The Development of Visual and Proprioceptive Control: A Whole- Body Perspective

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Abstract

Both the arms and the legs are crucial for everyday movement. Moreover, natural movement (like walking or dancing) frequently involves all four limbs simultaneously. However, our understanding of lower limb and whole-body sensorimotor control in children is limited because developmental research has traditionally focused on simple, single limb tasks (usually with just the arms). To address this, we investigated how children use visual and proprioceptive cues to perform both arm and leg movements, as well as complex, whole-body tasks.

Part 1 – Visual Control

In study 1, we showed that 6- to 8-year-olds rely on vision to the same extent as adults for stepping and reaching. However, stepping and reaching had different developmental profiles, with stepping error reducing between 6 and 8 years, whilst reaching error was stable. In study 2, 8-year-olds walked over stepping targets whilst we manipulated how many of the upcoming targets were visible. Children's foot placement error was higher than adults'. Nonetheless, children showed adultlike planning by slowing down and reducing error when they were unable to see at least 2 steps ahead.

Part 2 – Proprioceptive Control

In study 3, children attempted to remember and reproduce target arm and leg movements, following active (forward model generated) and passive (no forward model) target movement. Children performed poorly compared to adults and did not benefit from forward models. In study 4, we investigated whether children's whole-body proprioception and general movement skills could be improved by dance (relative to standard physical education or a non-movement control program). Despite finding no significant effect of dance on proprioception, we identified interesting inter-group differences and changes in sensorimotor skill over time.

Whole-body sensorimotor development is protracted and asynchronous. Upper and lower limb control have different developmental profiles and visual control matures before proprioceptive control. In the visual domain, children show sophisticated control strategies even before mature movement execution.

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Table of Contents

List of Figures

List of Tables

Declaration

The author confirms that none of the material presented in this thesis has been submitted elsewhere for any other qualification and is the author's own work unless referenced otherwise. This work was funded by the North East Doctoral Training Centre (Economic and Social Research Council, grant number ES/J500082/1) and was conducted in collaboration with Rachel Kurtz (Bare Toed Dance Company).

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Statement of Copyright

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Chapter 1

Introduction

Everyday movement is a whole-body phenomenon. When walking, dancing or simply getting dressed, we must move all four limbs in complex, coordinated action. Despite this, developmental research has focused on simple, single limb tasks and has often focused on the arms only. Consequently, we know very little about the development of lower limb sensorimotor control, or about the development of complex, whole-body movement. Do children use vision to guide precise stepping movements? Do children use visual information about the environment to plan ahead when walking in complex environments? What proprioceptive cues do children use to remember and reproduce arm and leg movements? Could we improve children's ability to remember and reproduce complex, whole-body positions through training? In this thesis, we address these questions to give a much needed whole-body perspective on sensorimotor development.

In this introduction, we outline the aims of the thesis, explain the importance of researching sensorimotor development, and expand on what we mean by a 'whole-body perspective'. We then outline the literature on sensorimotor control in adults and children, focusing on visual control and proprioceptive control. In discussing visual control, we outline how adults use vision to control stepping and walking, and introduce the more limited research on children's visually guided walking. We then outline research on adults' and children's visually guided reaching. Following this, we discuss two distinct types of visual control: online control and planning ahead. Finally, we explain the gaps in the visual control literature that are addressed in this thesis. In discussing proprioceptive control, we first describe proprioception in adulthood and then outline the developmental course of proprioception. Next, we introduce the concept of predictive mechanisms (forward models) in relation to proprioceptive judgements. We explain how we can experimentally manipulate the availability of forward models during proprioceptive tasks. We also introduce our whole-body approach to measuring proprioceptive awareness. Finally, we explain the gaps in the literature on proprioception that are addressed in this thesis. After detailing the literature on visual and proprioceptive control, we introduce the key methodological approaches and concepts used in this thesis: error, affordances and scaling, motion capture, and virtual reality. This is followed by a brief overview of the four experimental chapters: two studies focusing on visual control (part 1) and two studies focusing on proprioception (part 2). An introduction summary is given at the end.

1.1 Thesis Aims

The aim of this thesis is to describe sensorimotor development from a whole-body perspective. The studies presented in this thesis aim to determine the cues that children use to plan and control their movement and investigate how children's sensorimotor abilities change with age and experience. We address these aims through the two main areas: visual control (part 1), and proprioceptive control (part 2) of action.

1.2 Why Study Sensorimotor Development?

All behaviour is movement. Therefore, to study how children learn to use sensory information to control their actions is to study how children learn to behave in general. Fortunately, movements are directly observable (Adolph, Hoch, & Cole, 2018). Unlike cognitions, we can directly see, record and measure motor development. Further, motor development is enabling (Adolph & Hoch, 2019) - developments in the sensorimotor domain enable developments in other domains like language (Walle & Campos, 2014) and cognition (Gottwald, Achermann, Marciszko, Lindskog, & Gredebäck, 2016). Therefore, understanding how children learn to control their actions can help us support development in the motor domain and beyond. To study motor development (or development more generally), we need to appreciate its dynamic, non-linear nature.

Development is a dynamic system, influenced by the complex environment, the different experiences the environment presents, and the body, which is itself comprised of many components (Smith & Thelen, 2003). Both the environment and the body are rapidly changing entities, especially in childhood. As such, children must learn to use sensory cues about the complex environment and their own bodies in order to behave adaptively. The way in which children learn to control their movement in the complex environment is driven by numerous factors: cognition, balance, strength, body size, experience, sensory integration etc. Importantly, each of these components may have its own developmental trajectory which progresses in asynchrony from the other components (Kamm, Thelen, & Jensen, 1990). Consequently, development often follows a non-linear path, with qualitatively different strategies employed at different ages.

The development of visually-guided reaching is a particularly well documented example of non-linear development. At the newborn stage, infants demonstrate rudimentary hand-eye coordination; reaching for objects that they look at, but without successfully grasping or manipulating them (von Hofsten, 1982). This pre-reaching behaviour is ballistic and less accurate than the more controlled visually-guided reaching that emerges around 4 months (Bushnell, 1985). Once unimanual reaching is acquired, infants often show a return to bimanual reaching at walking onset, possibly to facilitate the acquisition of stable posture during bipedal locomotion (Corbetta & Bojczyk, 2002). The ups and downs of development continue in mid-childhood. At 5 years, children's target-directed reaches are ballistic and stereotyped: feedforward, or preprogramed in nature (Hay, 1979). But between 6 and 8 years, reaching error increases when vision of the hand is unavailable, suggesting that children increasingly rely on continuous visual feedback (Bard, Hay, & Fleury, 1990; Hay, 1979). After 8 years, error reduces again, with older children more flexibly integrating feedforward and feedback based strategies (Bard et al., 1990; Hay, 1979). From birth and throughout childhood, children's behaviour, strategies, and performance show distinct changes, sometimes returning to earlier strategies before moving onto a new one.

Crucially, this is not linear refinement of one particular reaching strategy. Rather, children move through a series of changing strategies across development. Because development is often non-linear and associated with qualitative change, it is not enough to measure abilities at the start point (infancy) and end point (adulthood). We cannot assume a smooth progression from one state to the other during childhood. Whilst the developmental profile of reaching has been extensively documented, the same is not true of other sensorimotor skills like stepping, walking, or proprioceptive judgements.

We also need to understand how particular experiences impact on children's sensorimotor development. Motor experience predicts motor development, more so than chronological age (Adolph, Vereijken, & Shrout, 2003). For example, infants given daily stepping practice show increased stepping behaviour relative to their peers (Zelazo, Zelazo, Cohen, & Zelazo, 1993); cultures which employ specific stretching and massage practices for infants see earlier walking onset (Hopkins & Westra, 1990). Once walking, development (e.g. longer, narrower, more consistent stepping) is most strongly predicted by the amount of walking experience (Adolph et al., 2003). The impact of different experiences on motor development highlights that children do not simply develop efficient, mature motor control without the necessary experiential input. Similarly, we know that by giving children specific experiences, we can improve their motor development. This opens the possibility to intentionally shape children's experiences to improve developmental outcomes. Mapping the developmental profile of sensorimotor skills allows us to understand when it might be appropriate and beneficial to introduce particular activities and experiences to benefit sensorimotor development. We need to understand when the developing system is flexible enough to explore and adopt new solutions to sensorimotor problems (Thelen, 1995).

1.3 The Whole-Body Perspective

This thesis examines development from a whole-body perspective. Much of the existing research on sensorimotor development uses tasks that involve only the arms, or only the legs. This stands in stark contrast to the whole-body nature of natural movement. Both the arms and the legs are crucial for everyday actions: reaching, grasping, holding, and manipulating objects with the arms; stepping, walking, jumping, sitting with the legs. Importantly, almost all activities involve the arms and legs simultaneously. For example, whilst walking, the arms swing in synchrony with the legs, we carry and manipulate objects with the arms whilst walking, and we use both the arms and the legs to steady ourselves if walking is interrupted. Experimental tasks that involve the whole-body (as per natural movement) may be more complex and challenging for children than heavily simplified single limb tasks. If we consider only simple, single limb tasks in isolation, we may overestimate children's sensorimotor skill.

Nonetheless, single limb tasks have their place for answering theoretical questions, even within a whole-body framework. Carefully controlled single limb tasks allow us to answer basic theoretical questions about how children use specific cues to control movements. Without this, we have little basis for designing and making predictions about more complex, whole-body tasks. Further, within a whole-body framework, single limb tasks allow us to compare performance of the arms and legs. Indeed, we might find differences between the arms and legs in both performance and developmental profile. In this thesis, we use a combination of single limb and whole-body tasks. In both part 1 (visual control) and part 2 (proprioceptive control) we begin with a simple, single limb task to identify the cues children use for sensorimotor control and to map the developmental profile of a sensorimotor skill. We then follow with a whole-body task to understand children's performance of a related, but more complex, naturalistic task. However, even in our single limb tasks, we test performance for both the arms and the legs.

1.4 Literature Overview - Sensorimotor Development

Human action control crucially depends on sensory input. This introduction focuses on action control using two key senses: vision and proprioception. We then discuss how these senses may be integrated.

1.4.1 Part 1 - Visual Control of Action

Vision and action are inextricably linked (Gibson, 1979). Through vision, we can determine and control our own direction of travel. Vision also provides information about the environment (obstacles, ground texture, depth changes) which we need to accommodate for safe and efficient movement. Vision informs us of both dynamic and stable properties of the world – it allows us to perceive moving objects (including our own body) and unmoving constants, like landmarks. Vision allows us to identify opportunities, goals, and constraints for movement. Reciprocally, movement allows us to gather even richer information about the world. As Gibson (1979, pg. 223) writes: "we must perceive in order to move, but we must also move in order to perceive". In the following paragraphs, we focus on how vision facilitates specifically the planning and control of stepping and walking.

In adults, visual information is used to fine-tune precise stepping movements and is also used to inform longer-term motor plans during walking. At the most basic level, visual input is used to fine-tune the trajectory of single stepping movements. If vision is occluded at the onset of a target-directed step, foot placement error increases (Reynolds & Day, 2005a). Error also increases if gaze is directed to the side of a stepping target (Smid & Den Otter, 2013). These results highlight that direct, visual fixation is beneficial. If a stepping target rapidly shifts position after a step has begun, the foot's trajectory can be rapidly adjusted (as early as 114ms after the target jump) to accommodate the change (Reynolds & Day, 2005b). In summary, continuous visual monitoring during precisely-placed single steps facilitates accurate performance in adults.

However, during walking we must make multiple steps in turn and accommodate environmental constraints and changes as we move. This calls for a different visual strategy. During walking, adults tend to fixate the next target in a sequence whilst the targeting foot is still on the ground, maintaining gaze on the target until 51ms (on average) after foot contact (Hollands, Marple-Horvart, Henkes, & Rowan, 1995). This behaviour suggests that adults plan ahead by visually sampling upcoming footfalls, but also have the possibility to update steps that have already been initiated. Indeed, adults visually sample upcoming targets (2 steps ahead) regardless of whether footfall targets are regularly or irregularly spaced (Patla & Vickers, 2003) and fixate obstacles in the walking path in the steps preceding but not during obstacle crossing (Patla & Vickers, 1997). Sampling of distal visual cues can facilitate adjustments to foot placement to accommodate obstacles (Krell & Patla, 2002), or can allow the walking pattern to remain consistent despite the presence of obstacles (Berard & Vallis, 2006). Adults' tendency to visually sample from a couple of steps ahead has been formalised and empirically supported in the critical control phase hypothesis proposed by Matthis and colleagues (Matthis, Barton, & Fajen, 2017), which is referred to in more detail later in this introduction and in chapter 3.

Of course, this sophisticated visual control of step placement and the planning of walking using distal visual cues must be learned. Nonetheless, even young infants make other types of locomotor decision which are sensitive and responsive to visual cues. At just 6- to 14-months, infants refuse to cross or show distress when faced with a large drop covered with clear glass – demonstrating an ability to sample and respond adaptively to visual environmental cues (Gibson & Walk, 1960). Toddlers also capitalise on visual sampling of the environment to make safe locomotor choices. For example, to safely slide down risky slopes, rather than walk (Adolph, Eppler, & Gibson, 1993), or to use handrails for steady crossing of narrow bridges (Berger & Adolph, 2003). However, infant visually guided locomotion does not have the same tight vision-action coupling of adult walking (Matthis et al., 2017). Walking infants do not always walk to specific, planned, visually-identified goals or locations. Instead, they walk around in an exploratory manner, happening across interesting objects along the way (Cole, Robinson, & Adolph, 2016).

But beyond infancy, children begin showing more adultlike visually guided precision in their walking. A small sample of children aged 4- to-8-years visually sampled obstacles a few steps in advance when walking in cluttered environments (Franchak & Adolph, 2010). Other studies show that children begin to use this visual information to tailor their behaviour. At 8 years, children use slower, wider steps in low light environments, and place their feet differently around the second obstacle of a series relative to a single obstacle (Berard & Vallis, 2006). This demonstrates more sophisticated planning using distal visual cues. Children of 8 years also adjust their step width when approaching obstacles, albeit to a greater extent than older children and teenagers (Corporaal, Swinnen, Duysens, & Bruijn, 2016). Between 9- and 18-years of age, variability of foot placement on stepping targets reduces, although foot placement accuracy is similar at all ages (Corporaal et al., 2018). These findings suggest that children as young as 8 years visually sample upcoming constraints, adjusting their motor plans effectively, but that there is continued refinement throughout adolescence.

Part 1 of this thesis focuses primarily on the visual control of stepping and walking but also of arm movements. Of course, arm movements are also guided by vision in both children and adults. Adults reach more slowly toward a target when vision of the hand and/or target is occluded (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996), adopting a more cautious approach when continuous visual monitoring is not possible. Similarly, the consistency of adults' reaches to a target decreases as the delay between viewing the target (which is subsequently occluded) and reach onset increases (Westwood, Heath, & Roy, 2003). Again, this suggests that memory of a target alone is not sufficient for precise reaching movements. Visual information is also crucial for the rapid updating of reaching movements. Visual changes in target location can evoke rapid updating of reaching movements within just 60 ms (van Sonderen, Gielen, & van der Gon Denier, 1989). In summary, adults use continuous visual input to make fast and precise target-directed reaching movements.

Although newborn infants can make rudimentary reaches, they must learn the precise visual guidance of arm movements. Newborns extend their arms toward visually fixated objects, although they do so quite clumsily (von Hofsten, 1982). By 4 months, a more controlled visually-guided reaching emerges (Bushnell, 1985). However, infants begin touching and grasping objects at similar ages both when the hand is visible (in the light) and when it is occluded (in the dark; Clifton, Muir, Ashmead, & Clarkson, 1993). This suggests that early reaching can be guided proprioceptively, without visual monitoring of the hand. Of course, for more fine-tuned, precise reaching, a robust visual monitoring system should be developed. By 6 years, target-directed reaches are significantly more accurate when continuous vision of the hand is available (Bard et al., 1990). In fact, between 6 and 8 years, removing visual feedback of the hand has an increasingly negative impact on accuracy (Bard et al., 1990). Thus, by mid-childhood, continuous visual input is crucial for target-directed arm movements.

1.4.1.1 Online Control and Planning Ahead. In this thesis, the terms 'online control' and 'planning ahead' distinguish between two temporal profiles of visual sampling during walking. In part 1 of this thesis, we are interested in whether children can engage in these types of visual control, which will now be described in more detail. A participant adopting a purely online mode of control will guide each step into place as the step occurs. The way this participant controls the current step will not be influenced by the upcoming terrain. In other words, they control their walking one step at a time. This type of online control is observed when adults walk in conditions of postural threat. For example, when walking on a raised walkway, adults demonstrate caution by focusing visual attention on the area of the walkway immediately in front of them (Ellmers, Cocks, Doumas, Williams, & Young, 2016; Ellmers & Young, 2019). Similarly, when making very precise steps toward a target, adults use continuous, online visual input to fine-tune the step trajectory throughout the movement, showing increased error when online vision is occluded (Reynolds & Day, 2005a; Smid & Den Otter, 2013). If the target location shifts after step initiation, adults can very rapidly redirect the foot's trajectory to accommodate the change (Reynolds & Day, 2005b). Again, this demonstrates adults' use of continuous visual input for guiding stepping movements. In study 1 of this thesis, we investigated whether children also use online visual feedback to fine-tune precise stepping movements and mapped the developmental profile of this skill between 6 and 8 years. We did so using a paradigm akin to that of Reynolds and Day (2005a). Participants made steps toward a target on the floor and we occluded vision at step onset on half of the trials.

However, when walking in complex environments, flexible and safe walking requires some planning ahead. Visual information about the upcoming terrain is needed to plan foot placement in advance. For example, given visual information about the upcoming terrain, adults may walk more quickly and place their feet more accurately (Matthis & Fajen, 2014). In fact, research has demonstrated a consistent relationship between visual sampling and foot placement in adults. Specifically, adults tend to visually fixate around 2 steps ahead (Hollands et al., 1995; Patla & Vickers, 2003). This consistent relationship between vision and foot placement was formally described by Matthis and colleagues in the critical control phase hypothesis (Matthis et al., 2017).

Central to the critical control phase hypothesis (Matthis et al., 2017) is the idea that walking should be energetically efficient. As far as possible, walking should be driven by passive forces of momentum and gravity, as if the body were a pendulum. The need for energetically costly, online adjustments should be minimal, since these require additional muscle activity. According to Matthis et al (2017), efficiency can be achieved by visually sampling from 2 steps ahead. This allows the walker to plan foot placement in such a way that the constraints of the upcoming terrain are accommodated, whilst also allowing the body to move forward largely ballistically. This hypothesis is supported by numerous experiments. Participants walking among virtual obstacles experience more obstacle collisions when visibility is restricted to less than 2 step lengths ahead (Matthis & Fajen, 2014). Increasing visibility to more than 2 steps ahead does not significantly benefit foot placement (Matthis & Fajen, 2014). When participants walk over a series of targets, foot placement error increases if a target is made invisible after initiation of the step to the preceding target (Matthis, Barton, & Fajen, 2015). Further, rendering a target invisible after initiation of the step to that target has little impact (Matthis et al., 2015). Together these results reinforce the precise, temporal coupling between vision and foot placement: adults preferentially visually sample from 2 step lengths ahead. In study 2 of this thesis, we explored whether children also use distal visual cues about the upcoming terrain to plan their walking. We did so using a paradigm akin to that used by Matthis and colleagues. Participants walked over a series of targets and we manipulated the 'window of visibility' to 1, 2 or 3 steps ahead.

In reality, naturalistic environments call for a combination of online control and planning ahead (Matthis, Yates, & Hayhoe, 2018). Matthis and colleagues recorded eye and body movements whilst adults walked outdoors in complex, natural terrain. They found that adults adjust their visual sampling strategy depending on the requirements of the terrain (Matthis et al., 2018). Participants looked more at the upcoming path in medium-rough terrains compared to flat. In medium-rough terrains, participants planned around 2 steps ahead, with gaze divided between 2 and 3 steps ahead in the roughest terrain. As terrain complexity increases, so does the need for forward planning, presumably as stable footholds become fewer. However, participants did also occasionally look at the immediate terrain, just one step ahead, as if engaging in online, feedback driven control. Despite all these changes in gaze behaviour, adults maintained a constant look-ahead time. They always looked to the location they would reach in around 1.5 seconds time, giving themselves time to make any necessary gait adjustments. In summary, Matthis et al (2018) show that in naturally complex environments, visual guidance of walking is changeable, but always driven by a need to plan ahead for both smooth forward progression and stability.

1.4.1.2 Filling the Gaps - Visual Control. The existing literature has comprehensively mapped the developmental profile of visually guided reaching. Research has detailed the shape of developmental change and the different strategies children use at different ages to control reaching movements. However, the same cannot be said of stepping. It is not clear whether children can use continuous visual feedback to fine-tune precise stepping movements, as adults do (Reynolds & Day, 2005a). Therefore, in study 1, we map the developmental profile of visually guided stepping and compare it to that of reaching. We measure children's precision stepping performance whilst manipulating the availability of visual feedback. The key research questions of study 1 are: do children use continuous visual feedback to guide precise stepping movements? And, does visually guided action develop in a limb-specific, or limb general manner? To answer these questions, we compare children's stepping and reaching performance with and without continuous visual input.

A rich body of literature on infant walking reveals that even young infants use visual cues in their environment to make appropriate motor decisions (Adolph et al., 1993; Berger & Adolph, 2003; Gibson & Walk, 1960). However, as discussed above, we cannot assume that development ends after infancy. Indeed, we know that other motor skills, such as reaching and balance, go through profound changes throughout childhood. A few studies have looked at visually guided walking in children (Berard & Vallis, 2006; Corporaal et al., 2016; Cowie, Atkinson, & Braddick, 2010; Cowie, Smith, & Braddick, 2010; Mowbray & Cowie, 2020). However, we do not have a clear understanding of how children control walking on long or complex paths. In particular, we know little about how children control their walking when the feet must be placed into very specific locations. Consider the example of walking on a rocky path – only certain locations on the path will allow secure foot placement and facilitate forward progression. In such a scenario, we do not know how accurately children can place their feet, or whether children use distal visual cues to plan foot placement in advance like adults (Matthis et al., 2017). Therefore, in study 2, we measure children's foot placement and speed as they walk over a series of targets. Crucially, we also manipulate how many of the upcoming targets can be seen (from 1 to 3 steps ahead). This allows us to determine whether or not children plan ahead using distal visual cues. The key research question of study 2 is: how do children use vision to control complex walking: do they plan ahead or guide each step one at a time?

1.4.2 Part 2 - Proprioceptive Control of Action

Vision alone is not enough to control the moving body. We cannot constantly visually monitor our whole body. Even when vision is available, two senses are better than one. We must also use proprioception; the sense of position and movement of the body, first defined in the early 20th century by Sherrington (1906). In short, proprioception is a sense of the bodily self. Signals from the skin, muscles and tendons about stretch and contraction provide us a sense of proprioception. We can begin to understand how crucial proprioception is for motor control by considering the effects of proprioceptive loss. Patients with sensory neuropathy (damaged sensory nerves) can experience proprioceptive loss. This can manifest in many ways that affect daily living, including: unstable gait or an inability to walk at all, poor balance, fine motor difficulties (e.g. problems buttoning clothes), difficulties detecting and/or localising touch on the body, and distorted movement trajectories when performing even simple gestures - all of which are often worse when vision is occluded (Sainburg, Poizner, & Ghez, 1993). These deficits give a sense of how important proprioception is for normal motor control. In contrast, healthy adults use proprioceptive feedback to guide precise movements and to accurately judge body position. Applying vibration to a tendon can disrupt proprioceptive feedback. When such vibration is applied to the bicep tendon, adults reaching without vision of the hand show a systematic directional bias (Redon, Hay, & Velay, 1991), suggesting that continuous proprioceptive input plays a key role in guiding arm movements. Adults can also successfully rely on proprioception to reach for an object in the dark (no visual feedback), albeit more slowly than in the light (Babinsky, Braddick, & Atkinson, 2012).

Interestingly, research suggests that proprioceptive accuracy is not equal for both sides of the body. Blindfolded adults can more accurately reproduce or match a target elbow angle when responding with their non-dominant arm (Goble, Lewis, & Brown, 2006). This asymmetry increases with increasing processing demand (e.g. matching contralateral limb position rather than ipsilateral) and larger elbow angles (Goble, Noble, & Brown, 2009). Goble et al suggest that this asymmetry could arise through experience of bimanual object manipulation. The non-dominant arm is typically used to hold still an object in a given position (using proprioception), whilst the dominant arm is used for manipulation (Goble et al., 2009).

Adult research on proprioception has also contributed to a wider literature on forward models. Forward models are generated in the cerebellum during active movement (Wolpert, Miall, & Kawato, 1998). They are predictions about the future state of the body, based on the current state of the body and active motor commands (Miall & Wolpert, 1996). The prediction can be compared against the actual motor outcome to produce an error signal, which can be used to update movement trajectories and subsequently improve predictions and motor accuracy (Miall & Wolpert, 1996). Blindfolded adults reproduce target movements more successfully following active target movement, compared to passive (Adamovich, Berkinblit, Fookson, & Poizner, 1998; Coslett, Buxbaum, & Schwoebel, 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko, Krouchev, & Kalaska, 2007; Laufer, Hocherman, & Dickstein, 2001). This suggests that both sensory feedback and feedforward cues contribute to adult proprioception.

But what about children? Is proprioception even present from infancy? Traditionally, we think of a sense of self emerging during the second year of life with mirror self-recognition (Amsterdam, 1972). However, younger infants do have a rudimentary sense of their own body position and movement. At just 5 months, infants demonstrate proprioceptive awareness. Bahrick and Watson (1985) and Schmuckler (1996) showed infants a video of i) their own movement (played live, synchronous with the infant's own movement), and ii) a non-synchronous video of their own movement or a different infant performing the same action. The infants in both studies showed a preference for looking at the non-synchronous display. Since their own moving limb was occluded during the experiment, this shows that the infants were able to map their own proprioceptive experience to the visual display. At 9- to 16-months infants reach similarly in the light compared to reaching in the dark (no vision of the hand) for a glowing object (Babinsky et al., 2012). And, at 7- to 21-months infants are equally successful at reaching to small vibrating targets on their face (not in visual field) or on their arm (in visual field), showing that they can combine tactile and proprioceptive information to guide reaching (Leed, Chinn,

& Lockman, 2019). This literature demonstrates that infants can use proprioceptive feedback about their arm position to guide movement when vision is not available.

In childhood, children continue to use proprioceptive feedback to guide their movement. When vibration is applied to the biceps muscle tendon, both 5- to 11-year-olds and adults show a systematic directional bias when drawing to a target (Hay & Redon, 1997). This effect is largest for the youngest children (Hay & Redon, 1997). This suggests that young children rely quite heavily on proprioceptive feedback. It may also suggest that older children additionally benefit from feedforward mechanisms (Hay & Redon, 1997). However, thus far, research has not directly tested whether children benefit from forward models on proprioceptive tasks in the same way that adults do. Further, proprioception may not be children's preferred sensory modality for position sense. von Hoftsen and Rösblad (1988) studied the cues that 4- to 12-year-olds use for position sense. Children used their unseen hand to point directly underneath a target presented on the table top. The target was specified visually (child sees target), visually and proprioceptively (child places their finger on the target, eyes open), only proprioceptively (child places their finger on the target, eyes closed), or from memory (target seen, then eyes closed). Overall performance improved with age, with most rapid improvements between 6 and 8 years for the proprioceptive and memory conditions. However, at all ages, children performed more accurately when the target was visually specified. These results suggest that primary school aged children are more adept at interpreting visual information than proprioceptive.

Developmental improvements in proprioception continue into adolescence. At 8- to 10-years, blindfolded children are less accurate and more variable than 16- to 18-year-olds at matching target elbow angles (Goble, Lewis, Hurvitz, & Brown, 2005). Like adults, 8- to 10-year-olds also show a non-dominant limb advantage in this task for the most complex conditions (matching with the contralateral limb from memory; Goble et al., 2005). Other work, using a similar elbow angle matching task, found no significant change in accuracy but a significant decrease in variability between 5 and 17 years (Holst-Wolf, Yeh, & Konczak, 2016). Despite slightly different results, both studies indicate that proprioception continues maturing throughout the adolescent years.

1.4.2.1 Forward Models. Proprioception is made up of both sensory feedback from the skin, muscles and tendons and from centrally-generated predictions (forward models). In this section we will explain the importance of these predictions for distinguishing between self-generated and externally generated movement or stimulation.

Movement of the visual world can mean two (non-mutually exclusive) things: i) movement of objects in the external environment, or ii) self-motion relative to the external environment (Gibson, 1979). Without an internal sense of self-motion, we cannot determine which explanation is true.

Proprioception tells us whether the body is moving or not, and how our body is positioned. The most obvious proprioceptive cue is sensory feedback: signals from the skin, muscles and tendons that indicate contraction and stretch. However, proprioception is also served by centrally-generated movement predictions: forward models. In the 19th century, Helmholtz observed that moving the eye passively (pressing gently without engaging the eye muscles) generated the false impression that the external world is moving (Wolpert & Flanagan, 2001). This led to the idea that under normal movement conditions, the brain does not just sense eye movements, but actually predicts them in a feedforward manner. This allows us to distinguish between self-movement and movement of the external world, or an external force (Wolpert & Flanagan, 2001). You can't tickle yourself for this very reason. Self-generated movements are predicted by the brain. Because they are predicted, their sensory consequences can be attenuated – hence why self-generated tickling doesn't work (Blakemore, Wolpert, & Frith, 2000). These feedforward predictions are referred to as forward models.

As well as distinguishing between self-generated and externally-generated movement, forward models contribute to accurate motor control. Forward models facilitate a more accurate estimate of the state of the body than could be achieved via sensory feedback alone. Sensory feedback is both noisy (subject to random error) and slow, subject to delays between a sensory event and registration in the brain (Wolpert & Flanagan, 2001). Feedforward predictions are made before movement onset. Therefore, they are not subject to the same delays as sensory feedback. However, the accuracy of such predictions will drift over time (Wolpert & Flanagan, 2001). To overcome these deficits, adults combine feedforward and feedback cues leading to a faster, more accurate estimation of the body's state (Wolpert & Flanagan, 2001). Adults also use feedforward and feedback mechanisms to facilitate motor learning via prediction errors. A forward model can be compared against the actual (sensed) outcome of a movement. A discrepancy between the predicted and the actual outcome (as indicated by sensory feedback) produces an error signal. This error signal can then be used to modify subsequent predictions and motor commands (Miall & Wolpert, 1996). If children struggle to produce, update, interpret or integrate forward models with sensory feedback, this will likely have a negative impact on their sensorimotor performance. Understanding whether or not children can benefit from forward models in the context of a proprioceptive task is the aim of study 3 in this thesis.

1.4.2.2 Manipulating Forward Model Availability. Adults use both sensory feedback and feedforward predictions for sensorimotor control (Miall & Wolpert, 1996). To understand the relative contribution of feedforward and feedback mechanisms, we need to measure sensorimotor performance whilst manipulating the availability of one of these cues. Previous work in adults has done this by comparing proprioceptive judgements under active (self-generated) and passive (apparatus-generated) movement conditions. During an active movement, a forward model prediction is generated (Miall & Wolpert, 1996) alongside sensory feedback. In passive movement, the movement cannot be predicted

– thus, there is no forward model, and only sensory feedback is available. Researchers have made such manipulations within a target and report paradigm. In the target phase, participants make an active or passive target movement. In the report phase, participants try to actively reproduce the target movement from memory. Findings consistently show that adults perform better following active movement (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). During the active target phase, the forward model can be activated and trained using sensory feedback. This allows for a more accurate movement in the report phase. Further evidence that this relates to forward models comes from research with patients who have damage to the cerebellum; the neural base of forward models (Wolpert et al., 1998). Cerebellar patients show poorer proprioceptive judgements than healthy controls in active, but not passive movement conditions (Bhanpuri, Okamura, & Bastian, 2013).

In study 3, we used a custom-built apparatus to administer active and passive movements. Participants held a handle or placed their foot on a foot plate. The hand or foot could then be actively pushed, or passively moved in the forwards-backwards plane. Importantly, the active and passive movements were identical in distance and trajectory. This meant that the sensory feedback was equated across both active and passive movements. We were also able to scale the movement amplitude to participants' body size, allowing valid comparison across participants of different sizes. In line with our whole-body approach, the apparatus allowed the task to be completed with either an arm or a leg, with distances scaled appropriately for each type of limb. This paradigm allowed us to directly manipulate the opportunity for forward model generation during a proprioceptive memory task in children in a way that previous research has not.

1.4.2.3 Measuring Whole-Body Proprioception. Many measures of proprioception are limited to testing just one limb at a time. Whilst single limb tasks have their place for addressing certain hypotheses, everyday movement involves coordinating the whole-body (multiple limbs simultaneously) in complex body shapes. In study 4, we devised a task which allows us to test whole-body proprioceptive memory. The participant lies on the floor, face up. The experimenter moves each of their four limbs into a pre-determined configuration. The participant must remember and reproduce this configuration after a short delay. We then measure error (in degrees) using large protractors placed underneath each of the participant's limbs. This low-tech, portable set up allowed us to conduct research in a school environment.

A similar method was used by Chatzopoulos and colleagues with pre-schoolers (Chatzopoulos, 2019; Chatzopoulos, Doganis, & Kollias, 2018). The participant's knee was moved (passively - moved by the experimenter) to a target angle. The participant then had to remember and reproduce the target angle actively. Performance on this single limb proprioception task improved among pre-schoolers following a program of creative dance (Chatzopoulos et al., 2018) and among 7-year-olds following a program of ballet (Chatzopoulos, 2019). This suggests that dance can be very beneficial for children's proprioception. However, Chatzopoulos et al's method tested only single limb proprioception, and only for the legs. Our method allowed us to test proprioception for whole-body postures, involving both the arms and legs simultaneously. This is a closer approximation of the demands of everyday movement which involves the whole body.

1.4.2.4 Filling the Gaps - Proprioceptive Control. A plethora of different tasks have been used to study proprioceptive development, providing a rich description of children's proprioceptive skill at different ages. However, there remain some significant gaps in the literature on proprioceptive development. Firstly, adult research has made broader contributions in terms of understanding the contribution of feedforward and feedback cues for proprioception. Adults make better proprioceptive judgements following active movement (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). This is thought to reflect the benefits of combining feedforward cues (generated in the brain during active movement) with sensory feedback. In contrast, the developmental literature has not yet used comparable paradigms to examine whether children also benefit from forward models for proprioceptive memory. To address this gap, in study 3 we assess children's ability to remember and reproduce target arm and leg movements. We manipulate whether the target movement is performed actively, or passively. This allows us to start to understand whether children benefit from forward models for proprioceptive memory. The key research question of study 3 is: do children benefit from forward models for proprioceptive memory? On a broader level, we also seek to map the developmental profile of memory-based proprioceptive judgements for both the arms and the legs.

Secondly, research has largely focused on arm movements, neglecting the legs. This is despite the legs being crucial for standing, walking, running, and dancing - all of which require sophisticated sensorimotor control. It is important that we adopt a whole-body perspective in sensorimotor research. Rather than assuming that sensorimotor development is limb-general, we should explore the possibility that upper and lower limb control may develop differently. In line with this, both studies 3 and 4 measure children's proprioception for both the arms and the legs. In study 3, we measure each limb separately. In study 4, we go further and ask children to remember and reproduce whole-body positions (involving all 4 limbs simultaneously). We view such a task to be more reflective of naturalistic movement demands. For this very reason, in study 4 we seek to improve children's whole-body proprioception by introducing a tailored creative dance program. The key research question of study 4 is: can children's whole-body proprioception be improved through dance? More broadly, this study assesses whether a very simple, low-investment intervention at school can have a meaningful impact on sensorimotor development.

1.4.3 Multisensory Integration

To understand sensorimotor control in detail, researchers often have to focus on vision and proprioception separately. This uni-sensory approach is taken in this thesis, where we focus separately on visual and proprioceptive control. In each of our experimental chapters, we manipulate just one sensory cue – for example manipulating the availability of visual information during stepping; or manipulating the availability of a forward model during a proprioceptive judgement task. However, we must acknowledge the importance of multisensory integration, since adults control their action using multiple cues – including vision, proprioception, and feedforward predictions. By using multiple sensory cues for action control, adults can behave flexibly when one or more cues is either unavailable or unreliable. Adults do this by weighting their reliance on each cue depending on its variability, placing greater weight on the most reliable cues (Nardini, Jones, Bedford, & Braddick, 2008). Poor sensory integration might be one reason why young children perform poorly on a range of sensorimotor tasks. As described in the following paragraphs, children do not optimally integrate multiple cues. Consequently, they must base sensorimotor decisions on a weaker evidence base than that available to adults. Poor sensory integration among children is a potential explanation for poor performance on many sensorimotor tasks, including those described in this thesis.

In a study by Nardini et al (2008) children (4- to 8-years) and adults collected glowing objects in a dark room and then attempted to return them to their original locations after a delay. The only external environmental cues to location were glowing landmarks. The other available cues were proprioceptive and vestibular cues related to the participants' own motion. The researchers compared three conditions: both landmarks and motion cues available, only motion cues available (glowing landmarks extinguished), and only landmarks available (participants motion-disorientated). Whilst adults performed most accurately given both landmarks and motion cues, children were no better in this condition than in either of the single cue conditions. In other words, children did not benefit from having multiple cues to object location. Instead, children tend to rely on one cue or another, switching between them rather than integrating them (Nardini et al., 2008).

Whether or not children integrate multisensory cues is partly dependent on their uni-sensory functioning. In a study by Nardini, Begus and Mareschal (2013), 7- to 9-year-olds, but not younger (4- to 6-years) or even older (10- to 12-years) children, performed more accurately on a proprioceptive judgement task when given both visual and proprioceptive information compared to either cue alone. However, at all ages, performance was improved with multiple cues available among those participants who had good proprioceptive accuracy. For those whose proprioception was no more than two times more variable than their vision, performance was better given multiple cues. Thus, younger children may struggle to integrate multiple sensory cues because the reliability of individual cues is still poor. For this reason, understanding the impact of manipulating a single sense (like vision or proprioception) on children's motor performance makes an important contribution to understanding children's performance on more complex multi-sensory integration tasks. In this thesis, we focus on vision and proprioception separately – but of course our findings may help to contextualise children's performance on other multi-sensory tasks.

1.4.4 The Development of Balance

In this thesis we focus on the development of visual control of stepping and walking, and on the development of proprioceptive memory for limb positions. Of course, there are many other facets of sensorimotor development. The development of balance control is particularly crucial, since it underpins the ability to perform almost all other actions in day-to-day activity. To stand and walk requires us to balance upright on two feet, even in the face of complex and changing terrains; to read or write requires a stable head and trunk to maintain visual focus on our task and to provide a stable base from which to move the arms. In line with our whole-body approach, it is important that we acknowledge the complex and crucial development of balance control.

Adults have sophisticated balance control which allows them to walk safely, even in very complex environments (such as a rocky path or a messy room). Adults can prevent falls when walking is interrupted by selecting footfalls which widen the base of support to promote stability (Moraes, Allard & Patla, 2007). Adults can also very rapidly adjust the trajectory of a step in response to changing visual information about the environment, even when balancing without support (Reynolds & Day, 2005b). Adults achieve this high level of skilled postural control by using multiple sensory cues – namely vision, proprioception and vestibular cues.

The importance of vision for balance can be demonstrated by measuring postural stability with and without visual input. For example, occluding vision leads to increased postural sway, even among highly trained dancers (Perrin, Deviterne, Hugel & Perrot, 2002). Therefore, even for dancers with extensive experience of balancing in unusual postures, vision remains crucial for stability. Other research compared the displacement of centre of pressure during standing in visually impaired and sighted adults - with eyes open and eyes closed. Visually impaired adults had poorer balance than sighted individuals only in the eyes open conditions (Sobry, Badin, Cernaianu, Agnani & Toussaint, 2014). This highlights the postural control advantage which vision affords sighted individuals.

Despite vision being very important for balance in adulthood, it is not on its own sufficient for optimum postural control – proprioception also plays a crucial role. This is starkly illustrated by the intense problems with balance and walking experienced by those with proprioceptive loss (Sainburg et al, 1998). In typical healthy adults, vision and proprioception are used together to control balance and adults weight their reliance on each sense depending on its reliability. For example, in the swinging room paradigm (Lee & Aronson, 1974), a large box is rotated in front of the participant to give the illusion of a swinging room, whilst the floor remains stable. This puts vision and proprioception in direct conflict - with vision suggesting movement and proprioception suggesting no movement. In this scenario, adults maintain relative stability by relying on proprioceptive input (Wann, Mon Williams & Rushton, 1998).

Vestibular cues are also essential for balance and must be used alongside visual and proprioceptive cues for greatest stability. The vestibular channel can be manipulated via Galvanic Vestibular Stimulation (GVS; the passing of an electric current through electrodes in the ears). This stimulation provokes a tilting of the head and body which is disruptive to balance. The reaction to GVS is far greater when other sensory cues are unreliable or unavailable (Day, Guerraz & Cole, 2002). Day et al (2002) demonstrated this increased GVS response in a patient with proprioceptive loss and in typical participants by manipulating the availability of visual information (the less the visual input, the greater the response to GVS). Once again, this highlights that for adults visual, proprioceptive and vestibular cues are used in concert to finely control posture and balance. The integration of multiple cues is key to a robust postural control system.

As we have already outlined in this introduction, sensorimotor control must be learned and developed throughout childhood. The development of balance control – like the control of reaching or stepping – is protracted and reliant on extensive experience. From the onset of standing, balance is crucial for preventing falls as infants learn to stand independently and later to walk. Human infants face a particular challenge, since they must balance on just two feet whilst also being top-heavy - having a large head relative to their body (Adolph, 2002). Even beyond the obvious challenges of balance during walking, postural control is crucial for supporting motor development more generally. In a sample of children aged 3- to 11-years, Flatters, Mushtaq, et al (2014) found that postural stability accounted for up to 10% of the variance in performance on fine-motor manual tasks. Good postural control allows for a stable base (stable head and stable trunk) from which to develop other crucial fine motor skills, such as handwriting (Flatters et al, 2014). Therefore, we must acknowledge the crucial role of balance as a foundational pillar of sensorimotor development. In the following paragraphs, we outline research on the sensory cues used by children for balance.

For young children, vision is the dominant sensory cue used for balance. At 13- to 16-months-old, infants sway, stagger or even fall when presented with a visual illusion suggestive of a swinging room – even when the standing surface is completely still (Lee & Aronson, 1974). The stable floor provides proprioceptive cues that the surface is not moving and adults use this to prevent swaying and falling (Wann et al, 1998). However, infants and nursery aged children are strongly reliant on visual cues and seem unable to switch to a proprioceptive control strategy (Lee & Aronson, 1974; Wann et al 1998). At 4- to 6-years, balance control remains immature. At this age, children sway significantly more than older children or adults even with full vision and a stable standing surface (Shumway-Cook & Woollacott, 1985). When standing with eyes closed, 4- to 6-year-olds sway even more, but remain standing (Shumway-Cook & Woollacott, 1985). However, when the standing surface is rotated to disrupt proprioceptive inputs, 4- to 6-year-olds are greatly destabilised. They struggle to stand when experiencing a rotated standing surface and visual occlusion together, leaving vestibular information as the only reliable cue (Shumway-Cook & Woollacott, 1985). In contrast, older children and adults maintain balance even in these challenging conditions (Shumway-Cook & Woollacott, 1985). These results highlight the fragility of postural control in young children and the difficulty they experience in using proprioceptive cues for balance – and even greater difficulty with vestibular cues.

Despite significant challenges in using vestibular cues to control balance, children do benefit from vestibular cues. De Kegel, Maes, Baetens, Dhooge & Van Waelvelde (2012) found that in a sample of 3- to 12-year-olds, performance on measures of vestibular function is an important predictor of motor performance, especially on balance tasks. In a study of 6- to 17-year-olds, Janky and Givens (2015) found that children with impaired vestibular function had poorer balance than their typical peers and that the extent of vestibular loss predicted performance on both static and dynamic balance tasks. Similar to adults, children's balance is impaired when vestibular inputs are disrupted or unreliable.

Nonetheless, balance remains immature into adolescence with heavy reliance on visual cues. At 11- to 13-years, visual occlusion has a much larger negative impact on postural stability for teenage girls than it does for adults (Blaszczyk & Fredyk, 2021). Similarly, 13- to 14-year-olds show higher sway than adults when tested in a variety of visual and proprioceptive conditions (Barozzi et al, 2014). Other research with professionally training male adolescent ballet dancers found that visual reliance for balance was lower at 14 years compared to 11 years, but increased again at 18 years (Golomer, Dupui, Séréni & Monod, 1999). The authors argue that a recent growth spurt could explain why 18-year-olds showed heightened visual reliance for balance. When the body grows rapidly, proprioceptive references are disrupted, leaving vision as the more reliable sensory input. This is partly why adolescence is generally viewed as a period of motor awkwardness (Quatman-Yates, Quatman, Meszaros, Paterno, & Hewett, 2012).

In summary, postural control poses a significant challenge to children. Children are predominantly reliant on visual cues for balance and experience high visual reliance even in adolescence. The development of postural control is protracted and complex. Although we do not focus on the development of balance in this thesis, we acknowledge the crucial role balance plays in almost all movement, from walking to writing. Immature balance could have an impact on children's ability to perform the types of task reported in this thesis. Therefore, in the experiments reported in this thesis, we measure or control for balance. In studies 1 and 2 on visually guided stepping and walking, we measure the balance ability of all participants and perform analyses to examine for relationships between balance performance and stepping performance. In both study 3 and study 4, we reduced any potential confounds of balance by having children perform proprioceptive tasks from a sitting or lying down position. Despite balance not being a core focus of this thesis, its pivotal role in movement is not to be ignored.

1.5 Thesis Methods and Approaches

In this section, we introduce the key methodological approaches used in this thesis.

1.5.1 Error

In each study we measure error. We use different types of error, each one providing a different insight into the participants' movement. Absolute error (accuracy) tells us how accurately a participant performs a movement. For example, can a participant land their step onto the very middle of a target? Constant error (bias) tells us about whether a participant performs a movement in a way that is biased in a particular direction. For example, does a participant consistently place their foot too far forwards or too far back relative to the target centre? Variable error (variability) tells us how consistently a participant performs a movement. For example, as a participant repeatedly steps toward a target, do they place their foot similarly from trial to trial? These error types are independent of each other. For example, a movement can have very low accuracy but high consistency. Further, these error types have the potential to show divergent developmental profiles. Importantly, we would not always expect all types of error to reduce over the course of development. Error is typically thought of as a negative variable, representing a mistake or immaturity. Indeed, excessive error of any type is likely to impede performance. However, the interpretation of error as a measure is a little more nuanced and depends on the specific questions being addressed.

Absolute error (accuracy) is perhaps the most intuitive error type. In real world terms, reducing absolute error is beneficial. For example, to reach a small object, guiding the arm accurately to the object's location is crucial in facilitating the object interaction. High absolute error might mean we miss the object all together. When walking on a rainy day, we must accurately guide the feet into dry spots on the pavement. High absolute error could mean that our feet get wet. Thus, absolute error is typically a negative variable: the higher the absolute error, the poorer the task performance. However, this does not mean that absolute error always reduces over development. Consider the developmental profile of reaching: mid-childhood has been cited as a period of higher absolute error relative to both older and younger ages (Bard et al., 1990). Therefore, whilst we typically seek to reduce absolute error for effective task performance, we cannot always assume a monotonic reduction in error to be the default in development.

Now let us consider constant error (bias). High constant error can go hand in hand with high absolute error. As we discussed above, high absolute error is usually a negative thing. However, biases can also be beneficial, or a marker of mature performance. For example, in a sensory adaptation task, participants make movements toward a target with visual feedback of the moving limb rotated relative to its veridical position. To reach the target successfully, participants need to learn a new mapping between their motor commands and the rotated visual feedback. The extent of learning on such a task can be measured using constant error. When the rotated visual feedback is removed, participants initially show after-effects: participants' movements are biased in the direction that was adaptive during visual feedback rotation (Kagerer & Clark, 2014). Here, constant error is a measure of successful sensorimotor remapping. Of course, if the constant error persists after the visual feedback rotation is removed, as can happen for young children (Kagerer & Clark, 2014), this is no longer adaptive. A second example comes from the walking literature. Walking adults' steps are biased to be longer and wider to avoid an obstacle, as opposed to shorter or narrower steps (Moraes, Allard, & Patla, 2007). Longer, wider steps offer more stability, which is a crucial safety consideration when walking is interrupted by an obstacle. Again, constant error is a measure of an adaptive strategy. Therefore, when we interpret measures of constant error, it is not simply a case of higher error signalling poorer performance. Rather, the specifics of our hypotheses and methods determine how we interpret this variable.

Variable error (consistency) typically reduces as we become more skilled at a given task (Vereijken, 2010). Being able to perform an effective strategy consistently is clearly beneficial. However, variable error can also be a positive and important part of development. Variability in performance is a natural and useful part of learning new motor skills (Adolph et al., 2018). Variability represents flexibility and adaptability (Vereijken, 2010). In fact, very low movement variability is a hallmark of atypical motor development (Hadders-Algra, 2010). Among typical children, those who show lower levels of movement variability when learning a motor task have poorer motor learning (Lee, Farshchiansadegh, & Ranganathan, 2017). Further, support for variability as a crucial part of motor learning comes from Ossmy et al (2018). In this study, simulated soccer-playing robots were movement trained using either basic, geometric paths, or using variable paths coded from videos of infant walking. The robots trained on infant paths won significantly more simulated games (Ossmy et al., 2018). In the real world, more variable movement allows a child to explore different possibilities for action and identify new ways of achieving a goal. With more experience, they can fine tune their strategy to the most effective one. By measuring variable error, we can observe, i) periods of developmental change, when children are exploring different possibilities for action and ii) periods of stabilisation, in which children settle into a more fixed strategy (Smith & Thelen, 2003; Thelen, 1995).

1.5.2 Affordances and Scaling to Body Size

Affordances can be thought of as possibilities for action that are presented by the fit between the actor and the environment (Gibson, 1979). Within a single environment, different bodies afford different actions. On the other hand, the same body affords different actions in different environments. For example, adults judge whether or not stairs can be climbed based on the riser height relative to their individual leg length (Warren, 1984). A set of stairs deemed to be climbable by a tall individual may be judged impossible by a smaller individual.

In childhood, the body changes rapidly. Children must tailor their movements to the capabilities of their body in the moment and meet the ever-changing demands of the environment (Adolph et al., 2018). Children must learn to not only perceive the properties of the environment, but to perceive the environment in relation to their own motor capabilities (Adolph, 1995). Even toddlers show some understanding of affordances. At the top of a slope, toddlers hesitate to visually sample and explore the slope through touch; they explore different positions for descent, and even refuse to descend slopes they deem too risky (Adolph, 1995). In other words, they select actions which represent an appropriate match between the environment and their abilities. However, even at 12 years, children make riskier choices than adults. For example, in a virtual cycling task 10- to 12-year-olds finished crossing intersections with less time to spare given the approaching traffic compared to adults (Plumert, Kearney, & Cremer, 2004), suggesting that even 12-year-olds overestimate their ability to cross the street quickly. Thus, affordances are continually fine-tuned throughout development.

But the key methodological consideration is: how to ensure that experimental tasks afford similar actions to participants of different sizes? Throughout this thesis, we compare the performance of children and adults. An experimental set-up designed for adults may not afford the same actions for children. A small step for an adult is a large step for a child. To address this, we scale our experimental tasks to the size of the participant. For example, we make the required step size proportional to leg length so that task difficulty is comparable across all participants. This means that the task has a similar level of difficulty for all participants, regardless of body size.

However, we do not scale the error data. Scaling error as the primary variable is not appropriate. If an adult with leg length 1m steps onto a target and lands 10cm off centre, unscaled error is 10cm. Error as a percentage of leg length would be 10%. If a child with leg length 50cm steps onto the target and also lands 10cm off centre, unscaled error is 10cm, as per the adult. However, error as a percentage of leg length is 20%, double that of the adult. If we consider error as a percentage of leg length, we would conclude that the adult was twice as accurate as the child. However, unscaled error shows that this clearly was not the case. When the task aim is to be as accurate as possible, it does not make sense to allow those with larger body dimensions a greater margin of error in absolute terms – providing the task difficulty is equated across participants. In a real-world scenario, greater error would result in missed footing and a fall, for example.

1.5.3 Motion Capture

In part 1 of this thesis (visual control of action), we use motion capture as our primary measure. Motion capture allows highly detailed and accurate measurements of both positional and temporal variables in much greater detail than visual observation alone. Observation can provide rich and interesting data on visually guided action. It can tell us whether or not participants are visually sampling environmental cues and whether they use visual input to make appropriate motor choices. For example, by coding whether infants succeed, fail, or refuse at descending a slope we can determine whether they are sensitive to visual cues about the environment and whether they over- or underestimate their walking skill (Adolph, 1995). However, this type of qualitative observational measure becomes increasingly difficult to implement with older participants who have relatively good motor control. For example, even with vision occluded, most typical adults and even children will successfully step onto a target to a more or less accurate extent. Thus, a simple success or fail measure would not be very informative. Without a detailed recording of foot placement, we would not be able to record the specific changes in error with age. Only through detailed motion capture analysis can we discover the small but important quantitative differences in foot placement between participants and between conditions. In the context of this thesis (part 1), we need highly detailed measurements of precision stepping.

1.5.4 Virtual Reality

In study 2, we measure walking behaviour in a complex environment using a combination of virtual reality (VR) and motion capture. For walking research, it is important that we use tasks that reflect the complex and cluttered real-world environment. Simple walking in a straight line is not reflective of real-world walking (Adolph et al., 2018). Using VR, we can easily manipulate the complexity of the walking task and environment. For example, we can create randomly spaced stepping stones and can easily manipulate how many of the upcoming stepping targets in a sequence are visible. As the participant steps onto the first target in the sequence, the next target can be triggered to appear. This approach is comparable to that used by Matthis et al (2017).

VR allows also us to manipulate postural threat whilst keeping all other aspects of the task identical and maintaining participant safety. For example, we compare walking on a flat walkway against walking on raised stepping stones in a pool of water. This is comparable to the approach taken by Ellmers and colleagues, who asked participants to walk on an elevated walkway (Ellmers et al., 2016; Ellmers & Young, 2019). VR is particularly useful when working with children. We can give the impression of walking on raised stones in water without increasing the actual risk to the participant. This would be of particular concern when working with children who do not have adultlike balance. Whilst harnesses could be used to ensure participant safety, the VR task allows participants to walk 'under threat' without the constraint or added weight of a harness.

Research suggests that despite some small differences between real-world and VR behaviour, the two are largely comparable. For example, wearing a head-mounted eye tracker (comparable to a VR headset) does not change the relationship between eye movements and body sway, even though body sway is reduced when participants wear a headset (Gotardi et al., 2020). Participants also scale their movements appropriately to the size of both real and holographic obstacles when stepping over them (Coolen, Beek, Geerse, & Roerdink, 2020) and maintain a similar margin of space between themselves and an obstacle whether it is real or virtual (Gérin-Lajoie, Richards, Fung, & McFadyen, 2008). In a study where participants did leave a larger clearance margin when walking around a virtual obstacle (vs. a real one), the difference in clearance margin was small at just 0.16 metres (Fink, Foo, & Warren, 2007). Further, only 40% of participants left a larger clearance margin for virtual obstacles (Fink et al., 2007). Participants may also walk more slowly in VR (Fink et al., 2007; Mohler, Campos, Weyel, & Bülthoff, 2007) and cross virtual obstacles with lower peak foot acceleration compared to real obstacles (Ida, Mohapatra, & Aruin, 2017). Nonetheless, small quantitative differences between real and VR behaviour do not negate the validity of VR experiments. We can still draw valid conclusions about relative differences between groups of participants within a single virtual environment. And, since the behavioural differences between real and VR behaviour are both small and quantitative, we can make inferences about real-world behaviour from VR task performance.

1.6 Experimental Chapters

This thesis focuses on two key areas: part 1 focuses on visual control (studies 1 and 2), and part 2 focuses on proprioceptive control (studies 3 and 4). In both part 1 and part 2, we begin with a simple, single limb task (performed separately with the arms and the legs; studies 1 and 3). We follow this with a more complex but closely related whole-body task (studies 2 and 4). The following sections briefly introduce the background and aims of each of the four experimental studies.

1.6.1 Part 1- Visual Control of Action

1.6.1.1 Study 1 – The Development of Visually Guided Stepping. A large body of research has detailed the developmental profile of visually guided reaching. In mid-childhood (around 8 years) visually guided reaching undergoes a transition, during which reaching becomes slower and less accurate than at younger or older ages (Bard et al., 1990; Hay, 1979; Hay, Bard, Fleury, & Teasdale, 1991; Pellizzer & Hauert, 1996; Van Braeckel, Butcher, Geuze, Stremmelaar, & Bouma, 2007). However, existing research has not provided an equally detailed account of stepping development. The aim of study 1 was to establish whether stepping would be visually guided and whether it would have a similar developmental profile to reaching. We investigated this among 6-, 7-, 8-year-olds and adults using motion capture to record steps and reaches made both with and without continuous visual feedback.

1.6.1.2 Study 2 – Children's Walking in Complex Environments: One Step at a Time? Despite being crucial for fluent movement, the influence of visual information on where children place their feet during complex walking has not been extensively investigated. Adult research shows that adults consistently visually sample from around 2 steps ahead, both when stepping on targets and when crossing or avoiding obstacles (Hollands et al, 1995; Matthis & Fajen, 2014; Matthis et al., 2015; Patla & Vickers, 2003; Patla & Vickers, 1997). Although children visually fixate obstacles a few steps ahead of obstacle crossing (Franchak & Adolph, 2010) and adjust foot placement to accommodate upcoming obstacles (Berard & Vallis, 2006) we do not know if children show a tight and consistent temporal coupling between vision and action during walking, as adults do. The aim of study 2 was to establish whether children use visual cues to plan ahead during walking or adopt a more online mode of control. We were also interested in how their strategy might change under conditions of postural threat. We investigated this using an immersive VR paradigm.

1.6.2 Part 2 – Proprioceptive Control of Action

1.6.2.1 Study 3 – The Development of Forward Models for Proprioception. Adult research has consistently shown that adults make better proprioceptive judgements following active movement, for which a forward model is generated (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). However, this work has narrowly focused on arm movements and does not have a parallel developmental literature. Developmental work has not clearly established whether children are using feedforward or feedback cues to make proprioceptive judgements. The aim of study 3 was to investigate whether children benefit from forward models for memory-based proprioceptive judgements. We did this by directly manipulating the opportunity for forward model generation during movements in children using active and passive movement.

1.6.2.2 Study 4 – Can Dance Improve Children's Proprioception? Young children have relatively poor proprioception (Contreras-Vidal, 2006; von Hoftsen & Rösblad, 1988) and mature proprioception is not achieved even in adolescence (Holst-Wolf et al., 2016). Furthermore, most existing research uses simple, single limb tasks which might even overestimate children's abilities. Since proprioception is crucial for everyday motor control, it would be useful to improve this sensorimotor skill in children. Dance is a promising candidate for improving proprioception. Professional dancers have superior proprioception to non-dancer controls (Golomer, Crémieux, Dupui, Isableu, & Ohlmann, 1999; Jola, Davis, & Haggard, 2011; Kiefer et al., 2013) and previous studies show that dance training can improve children's single limb proprioception (Chatzopoulos, 2019; Chatzopoulos et al., 2018). The aim of study 4 was to establish whether a tailored school-based dance program could improve complex, whole-body proprioception in school children, using a non-randomised control design.

1.7 Introduction Summary

The aim of this thesis is to describe sensorimotor development from a whole-body perspective. We studied control of the arms and the legs, and used complex, whole-body tasks to explore both quantitative and qualitative changes in sensorimotor strategy across development. In part 1, we map the little-researched developmental profile of visually guided stepping and test children's visually guided planning strategy during complex walking. In part 2, we investigate whether children use feedforward cues for proprioceptive judgements and measure children's ability to make whole-body proprioceptive judgements, before and after dance training. Together, these studies address broader questions about whether sensorimotor control develops in a limb-general or limb-specific manner, and about the overall shape of sensorimotor development.

Part 1 – Visual Control

Chapter 2

Study 1 - The Development of Visually Guided Stepping

2.1 Introduction

For safe walking in complex environments, foot placement must be guided by visual cues about obstacles, depth and ground texture. However, infants are not born able to make controlled, precise, visually guided steps. Independent standing and functional steps are not available for many months. However, by toddlerhood children accumulate vast and varied walking experience (Adolph et al., 2012) and by 4 years, there is some evidence of adultlike visual behaviour during walking (Franchak & Adolph, 2010). However, little research has directly tested how well children use this visual information to guide precise stepping. As a starting point, we look to the extensive literature on children's visually guided reaching as a model of visually guided action.

2.1.1 The Development of Precision Stepping - Insights from Reaching

For reaching, there is a mid-childhood transition (Bard et al., 1990; Hay, 1979; Hay et al., 1991; Pellizzer & Hauert, 1996; Van Braeckel et al., 2007). Eight year old's reaches are less accurate and slower than younger or older children's (Bard et al., 1990; Hay et al., 1991; Pellizzer & Hauert, 1996). Young children process visual and proprioceptive inputs relatively separately (Chicoine, Lassonde, & Proteau, 1992). In mid childhood, children begin integrating these inputs (Hay, 1979; Van Braeckel et al., 2007). However, cortical regions associated with sensorimotor integration mature later than motor and sensory systems (Lenroot & Giedd, 2006), causing a brief increase in reaching error.

Stepping might develop as part of broader sensorimotor development and, like reaching, show non-linear development. Adults' steps and reaches have similar kinematic profiles and visual control mechanisms. They share a two-phase speed profile (Berthier & Keen, 2006): first an acceleration phase brings the effector to the relevant area, then a deceleration phase for visually guided fine-tuning (Jakobson & Goodale, 1991; Reynolds & Day, 2005a; Zhao & Warren, 2015). Adults rapidly update steps and reaches in response to visual change (Pisella et al., 2000; Reynolds & Day, 2005b) and without vision, both steps and reaches are slower and less accurate (Babinsky et al., 2012; Berthier et al., 1996; Reynolds & Day, 2005a; Smid & Den Otter, 2013; Westwood, Heath, & Roy, 2001).

Given the similar visual guidance of adults' steps and reaches, we might also expect similarities in childhood. Starting with reaching, newborns make predictive arm movements to moving objects (von

Hofsten, 1980, 1982). Nine month olds' reaches are kinematically different when vision is occluded (Babinsky et al., 2012). In mid childhood, reaching is less accurate without vision (Bard et al., 1990). For stepping, infant step frequency increases with visual stimulation (Pantall, Teulier, Smith, Moerchen, & Ulrich, 2011) and 3 year olds rely on visual depth cues to control step descent (Cowie, Atkinson, et al., 2010). Like reaching, stepping (e.g. in the context of obstacle crossing) remains immature in mid-childhood (Berard & Vallis, 2006). But can children use online vision to fine-tune precise steps to a target? This visually guided precision is crucial for walking in natural environments (Chapman & Hollands, 2007; Matthis et al., 2018).

The neural control of precise, visually guided action may be limb-general. The neural mechanisms of reaching may even have evolved from those controlling quadrupedal locomotion (Georgopoulos & Grillner, 1989). Parietal regions control visually guided action in an effector-general manner (Tunik, Rice, Hamilton, & Grafton, 2007) and control the planning of upper (Buneo & Andersen, 2006) and lower limb movement (Drew, Andujar, Lajoie, & Yakovenko, 2008; Gwin, Gramann, Makeig, & Ferris, 2011). Precise stepping also engages prefrontal areas (Koenraadt, Roelofsen, Duysens, & Keijsers, 2014) and is negatively affected by cognitive load (Alexander, Ashton-Miller, Giordani, Guire, & Schultz, 2005). However, we lack developmental evidence. Again, we look to reaching for clues: executive function correlates with reaching behaviour in infancy and childhood (Gottwald et al., 2016; Ruddock et al., 2016; Wilson & Hyde, 2013). Given these ties between cognition and action and the protracted development of frontal regions (Blakemore & Choudhury, 2006; Gogtay et al., 2004), we might predict that visuomotor development is overall long and driven by cognitive development.

2.1.2 Stepping and Reaching Might Have Different Developmental Profiles

Despite the above-discussed similarities, developmental motor assessments commonly treat upper limb tasks, like grasping and reaching (fine motor) as qualitatively distinct from gross motor skills, like walking and balance (Cools, Martelaer, Samaey, & Andries, 2009). Futher, the hands and feet are represented in distinct neural areas (Bracci, Ietswaart, Peelen, & Cavina-pratesi, 2010; Dall'Orso et al., 2018). However, neural body representation tells us little about movement control. During adult movement, the neural coupling of the arms and legs is task dependent (Volker Dietz, 2002, 2018; Frigon, 2017). For skilled, visually guided action, the arms are controlled by direct cortical-motoneuronal connections independently of the legs (Dietz, 2003) but this does not necessitate asynchronous development of stepping and reaching.

Nonetheless, stepping and reaching do emerge at different times. Within months, infants can reach from a sitting posture (Thelen & Spencer, 1998). Purposeful stepping, on the other hand, comes later. Infants must stand independently, before then learning to step in ways which promote stability

(Moraes, Lewis, & Patla, 2004; Roncesvalles, Woollacott & Jensen, 2000) and to adjust active steps for careful foot placement. This poses a huge demand, given that balance remains immature long after walking onset (Brenière & Bril, 1998; Godoi & Barela, 2008; Woollacott & Shumway-Cook, 1990). Nonetheless, just like stepping, reaching is crucially reliant on postural control. An infant must be able to stabilise the head and shoudlers before they can reach successfully (Thelen & Spencer, 1998). They must also develop anticpatory postural adjustments to support reaching (Witherington et al., 2002). In older children, postural stability correlates with manual dexterity (Flatters et al., 2014). Postural contol is not a unique requirement of stepping – it underpins action more broadly.

In sum, evidence suggests that stepping and reaching are more similar than different. Both are visually guided in adulthood (Babinsky et al., 2012; Reynolds & Day, 2005a), with similar kinematic profiles (Berthier & Keen, 2006; Reynolds & Day, 2005a), similar neural control mechanisms (Buneo & Andersen, 2006; Drew et al., 2008; Tunik et al., 2007) and ties to cognition (Alexander et al., 2005; Gottwald et al., 2016) and postural stability (Flatters, Mushtaq, et al., 2014; Moraes et al., 2004). Further, both reaching (Bard et al., 1990; Hay et al., 1991; Pellizzer & Hauert, 1996) and stepping (Berard & Vallis, 2006), remain immature in mid childhood. Together, this evidence indicates that visually guided stepping and reaching might have similar developmental profiles.

2.1.3 How Might We Measure Stepping Development?

To understand the development of precision stepping, we measured three different error types. Absolute error indicates the accuracy with which an individual can bring their effector to the target. Without vision, absolute error is increased for adult steps (Reynolds & Day, 2005a). Variable error tells us how consistent steps are from one attempt to the next. Whilst variability tends to reduce with experience, it is an important feature of the learning process (Gliga, 2018; Lee et al., 2017), allowing exploration of possibilities for action. Like absolute error, when vision is occluded, variability increases for adult steps (Reynolds & Day, 2005a). Constant error (directional bias) might be particularly relevant for stepping. Adults preferntially step in ways that promote stability, widening or lengthening the base of support (Moraes et al., 2004). In other cases, constant error may represent maladaptive perceptual or response biases (Smid & Den Otter, 2013). By considering multiple errors, we can address multiple hypotheses.

To our knowledge, this is the first study to map the development of visually guided precision stepping on flat ground. With children and adults, we manipulated visual input during steps and reaches in two directions. We hypothesised firstly, that both steps and reaches would be visually guided (H1), with greater absolute and variable error with vision occluded (Chicoine et al., 1992; Cowie, Atkinson, et al., 2010). Secondly, that stepping develops as part of broader visuomotor development, sharing a developmental profile with reaching (H2) with increased absolute and variable error in mid childhood (Bard et al., 1990; Hay et al., 1991; Pellizzer & Hauert, 1996; Van Braeckel et al., 2007). Thirdly, that step error would be affected by step direction (H3), with greater error for side steps, especially without vision (Reynolds & Day, 2005a). We also expected side steps to be widened and straight steps lengthened, widening the base of support (Moraes et al., 2004). Finally, regarding postural stability (H4), we hypothesised that stability would correlate with step error, improve with age and be poorer without vision (Woollacott & Shumway-Cook, 1990).

2.2 Methods

2.2.1 Participants

All participants gave informed consent and had typical cognitive, motor and physical development, normal or corrected to normal vision and right hand and foot dominance. For handedness and footedness participants/parents were asked which hand they/their child write(s) with and which foot they/their child normally kick(s) a ball with. We verified binocular depth perception in all participants with the Frisby stereo test (Frisby, 1980).

Six year olds (N=11, 5 female) had a mean age of 5.9 years (SD=0.2 yrs), mean leg length of 58.6 cm (SD=2.9cm) and mean arm length of 49.6cm (SD=2.7cm). Seven year olds (N=11, 3 female) had a mean age of 6.9 years (SD=0.1 yrs), mean leg length of 61cm (SD=4.32cm) and mean arm length of 52.8cm (SD=2.4cm). Eight year olds (N=11, 3 female) had a mean age of 7.9 years (SD=0.4 yrs), mean leg length of 68.1cm (SD=4.2cm) and mean arm length of 55.6cm (SD=2.6cm). Adults (N=15, 10 female) had a mean age of 25.9 years (SD=3.4 yrs) and mean leg length of 88.3cm (SD=6.0cm).

2.2.2 Design and Equipment

Children completed the reaching task and the stepping task (order counter-balanced). Adults completed the stepping task only. The development of visually guided stepping has been less extensively researched than the visual control of reaching, making an adult comparison group important for interpreting children's step error. Both reaching and stepping tasks used a mixed design with two within-subjects variables: vision (on/off) and direction (ahead/side) and one between-subjects variable: age (6/7/8 years/adult). These age groups would allow us to identify an increase in error between 6 and 8 years (Bard et al., 1990; Hay et al., 1991).

We used Vicon motion-capture (240Hz) with reflective markers on participants' bare right foot on the second metatarsal head, front ankle, lateral malleolus and heel. For reaching, there was a single marker on the right index fingernail. To measure postural control, one marker was placed on each shoulder. Participants wore PLATO glasses throughout, allowing visual occlusion via a button press. We chose reach and step distances via piloting in which participants made a self-determined comfortable step/reach. Steps of 45% leg length, and reaches of 30% arm length were consistently deemed comfortable.

For stepping, we marked start positions by tracing around the feet. We made step targets by cutting out a card trace of the participant's right foot. We measured participants' leg length from anterior superior iliac spine (pelvis) to medial malleolus (inner ankle). Required step length was scaled to leg length by sorting leg length into bands (Band 1 >30cm<=49cm, Band 2 >=50cm<=69cm, Band 3 >=70<=89, Band 4 >=90cm<109cm) and scaling according to the average length for that band. We secured targets to the floor with Velcro: one target 45% leg length straight ahead of the right foot start position, the second target 45 degrees to the right, also at a distance of 45% leg length. For example, a leg length of 62cm falls into Band 2 (for which average leg length is 60cm), which required step distance of 18cm (45% of 60cm).

For reaching, a start position for the right index finger was marked by a star sticker on the table top. Star targets (diameter=13mm) were also placed on the table top. We measured participants' arm length from shoulder to the end of the middle finger and scaled required reach length by sorting into bands (Band 1 >40cm<=49cm, Band 2 >=50cm<=59cm, Band 3 >=60cm<=69cm, Band 4 >=70cm<80cm) as per leg length. We placed one target 30% arm length, straight ahead of the right finger start position. The second target was placed 45 degrees to the right, also at a distance of 30% arm length.

2.2.3 Procedures

To measure postural stability, participants stood with feet shoulder width apart and were instructed to stand as still as possible for 30 seconds, then again with vision occluded. For the main task, participants made reaches/steps to targets with and without vision. For stepping, participants began standing on the start positions. For reaching, participants were seated with their right index finger on the start position. On each trial, the experimenter covered one of the targets (ahead or side) using card which was colour-matched to the surface.

For both steps and reaches, we asked participants to move in time with an audio track. This was 4 rhythmic tones, followed by the vocal: "drip, drop splash!" (tones/words *M*=655ms apart). Participants were required begin their step/reach on "drop", land it onto the target on "splash" and then return to the start position. For stepping, we instructed participants to match their own foot exactly to the target foot. For reaching, we instructed participants to point to the middle of the target. The audio track was played on loop with a 7 second delay between trials, during which the experimenter set up the next trial by covering one of the targets. We instructed participants to look at the visible target ready for the next trial. In the vision off condition, we occluded vision on the word "drop", which coincided with movement onset, until the step/reach was complete. The only difference between the visual conditions was the availability of vision *during* the movement. Participants completed 4 blocks of 10 trials for both steps and reaches in which conditions were randomised, with short breaks as needed.

2.2.4 Analysis

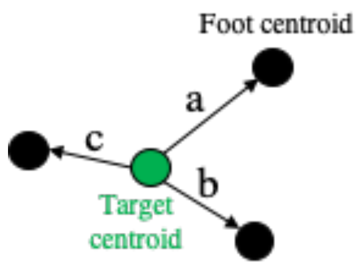

Figure 2. 1. Error types. For step and reach error we calculated 3 error types. Constant error: e.g. signed mean value of distances a, b and c. Absolute error: e.g. unsigned mean value of absolute distances |a|, |b| and |c|. Variable error: e.g. standard deviation of absolute distances |a|, |b| and |c|.

We recorded the locations of the start position and targets using motion capture. We filtered motion capture data using a 6Hz low-pass Butterworth filter. A custom-written MATLAB script calculated the centroids of the start position and targets. The centroid (or centre of mass) of a shape is the mean position of all coordinates in the shape. We calculated error using the distance between the target centroid and foot/finger centroid at the end of the step/reach (Figure 2.1). To analyse postural stability, we calculated path length of the shoulder markers: mean distance (in any direction along the medial-lateral and anterior-posterior axes) moved by the shoulder markers. We analysed the dependent variables using mixed model ANOVAs and Bonferroni-corrected post hoc tests. We calculated partial correlations between shoulder path length and absolute error for both steps and reaches, controlling for age. Due to kurtosis in the data, we transformed the stepping, reaching and postural data by taking the square root of the values before calculating correlations.

We excluded trials where the participant did not do the task as instructed (e.g. used the left foot) or because of equipment error (e.g. PLATO glasses batteries were flat). For stepping: no adults had trials excluded. Three 6 year olds had 1 trial excluded and one 6 year old had 3 trials excluded. One 7 year old had 1 trial excluded, one had 2 trials excluded and one had 7 trials excluded. One 7 year old was excluded from the stepping and reaching analysis entirely since they had 11 trials excluded (>25% stepping data). One 8 year old had 1 trial excluded. For reaching: one 6 year old had 2 trials excluded and one had 3 trials excluded. Two 7 year olds had 1 trial excluded and one 7 year old had 5 trials excluded. One 8 year old had 1 trial excluded.

2.3 Results

For stepping, shoulder path length and reaching, we report main effects of vision, age and direction on: absolute, variable and constant error. There was only one significant interaction between vision and direction for variable step error. We also present correlations between step error, reach error, and shoulder path length. We reiterate our hypotheses: H1 – steps and reaches will be visually guided, with higher absolute and variable error when vision occluded; H2 – stepping and reaching will share a developmental profile, with a mid-childhood peak in absolute and variable error; H3 – step error will be affected by step direction, with higher error for side steps with vision occluded and a bias to widen the base of support; H4 – step error will correlate with postural stability.

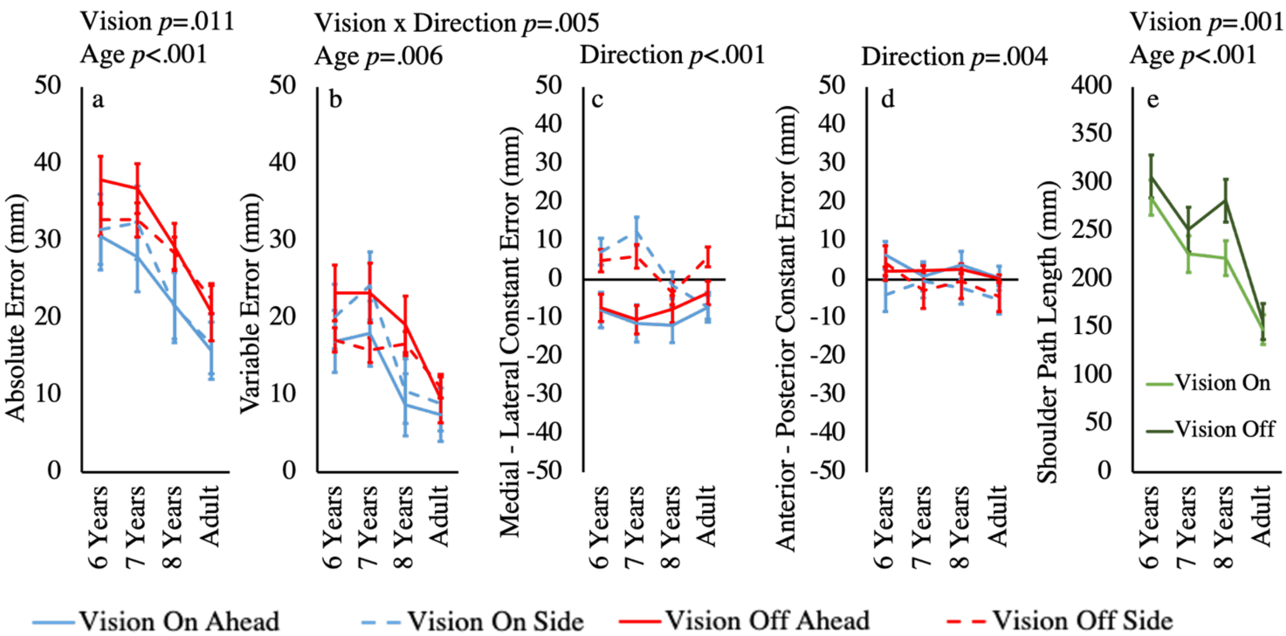

Figure 2. 2. Step error and postural stability. Group means for absolute error (a); variable error (b); constant medial-lateral error (c); constant anterior-posterior error (d); and shoulder path length (e). Values are shown for both vision conditions (on/off) and both directions (ahead/side) at all ages. For medial-lateral error (c): negative values indicate left bias, positive values indicate right bias. For anterior-posterior error (d): negative values indicate backward bias, positive values indicate forward bias. Error bars show standard errors. Significant main effects and interactions are listed (with p values) at the top of each sub-plot.

In support of H1, absolute step error was significantly higher with vision occluded (M=30.1mm, SE=1.0mm) than with vision available (M=24.7mm, SE=2.0mm) $F(1, 43)=7.125$, p=.011, ηp^2=0.142

(Figure 2. 2a). There were significant effects of age on absolute step error $F(3, 43)=8.079$, $p<.001$, $\eta p^2=0.36$ (Figure 2. 2a). However, contrary to H2, we did not find any increase in error in mid-childhood. Rather, children's absolute step error was higher than adults' (M=18.9mm, SE=2.2mm) at 6 years (M=33.2mm, SE=2.5mm, p=.001) and 7 years (M=32.5mm, SE=2.7mm, p=.002) with no significant difference in absolute step error between 6 and 7 years (p=1.00). By 8 years (M=25.2mm, SE=2.5mm), absolute step error was adultlike (p=.413). The reduction in absolute step error between 7 and 8 years was not significant (p=.326). This effect of age cannot be explained by better task learning among older children and adults: we found no overall change in error between the first and last 5 trials (p=.141) and no interaction with age (p=.364). Contrary to H3, there was no effect of direction on absolute step error (p=.793).

Our results for variable step error partially support H1. Whilst, there was no main effect of vision on variable step error (p=.099), there was a significant interaction between vision and direction $F(1, 43)=8.559$, $p=.005$, $\eta p^2=0.116$ (Figure 2. 2b). For steps straight ahead, variable error was higher with vision occluded (M=30.8mm, SE=1.8mm) than with vision available (M=23.2mm, SE=2.2mm) $t(46)=-3.547$, $p=.001$. For side steps, there was no effect of vision (p=.099). Therefore, H1 is largely supported, but qualified by step direction. There was a significant effect of age on variable step error $F(3, 43)=4.813$, $p=.006$, $\eta p^2=0.251$ (Figure 2. 2b). However, contrary to H2, post hoc tests did not reveal any significant differences between any of the child age groups for variable error (p*'s* >.3): 6 years (M=19.4mm, SE=2.6mm), 7 years (M=20.9mm, SE=2.7mm), 8 years (M=13.8mm, SE=2.6mm). However, variable error was generally higher in children, and significantly higher for 6 year olds than adults (p=.029). There was no effect of direction on variable step error (p=.593).

There was no effect of vision or age on constant step error (p*'s*>.5). In support of H3, there was a significant effect of direction on medial-lateral constant step error $F(1, 43)=26.447$, $p<.001$, $\eta p^2=0.381$ (Figure 2. 2c) and on anterior-posterior constant step error $F(1, 43)=9.230$, $p=.004$, $\eta p^2=0.177$ (Figure 2. 2d). Participants had a medial bias in the ahead condition (M=-8.4mm, SE=1.7mm) and a lateral bias in the side condition (M=3.9mm, SE=1.7mm). Steps were biased forwards in the ahead condition (M=2.3mm, SE=1.0mm) and backwards in the side condition (M=-1.9mm, SE=1.8mm).

As predicted (H4), shoulder path length was significantly greater with vision occluded (M=249.2mm, SE=10.69mm) than with vision available (M=220.4mm, SE=8.9mm) $F(1, 43)=12.160$, $p=.001$, $\eta p^2=0.220$ (Figure 2. 2e). Also confirming H4, there was a significant effect of age on shoulder path length $F(3, 43)=12.923$, $p<.001$, $\eta p^2=0.474$ (Figure 2. 2e). Children of all ages (6 years - M=296.0mm, SE=18.2mm, p=<.001; 7 years - M=239.2mm, SE=19,3mm, p=.007; 8 years - M=252.0mm, SE=18.2mm, p=.001) had greater shoulder path length than adults (M=152. 2mm, *SE*=15.6mm). Contrary to H4, shoulder path length did not correlate with step error in any condition (*p*'s> .09).

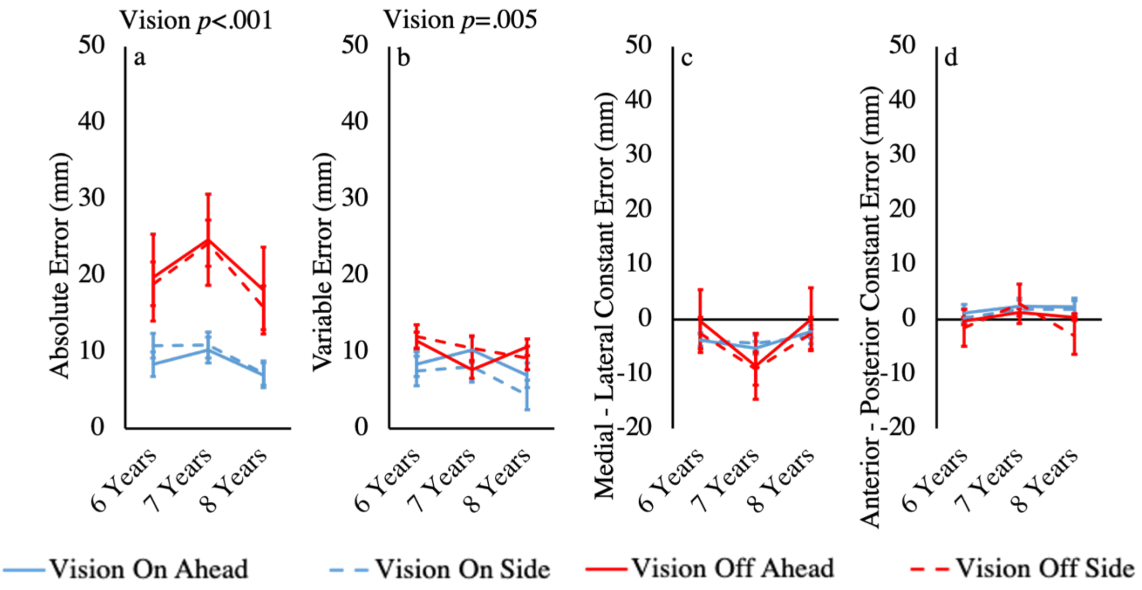

Figure 2. 3. Reach error. Group means for absolute error (a); variable error (b); constant medial-lateral error (c); and constant anterior-posterior error (d). Values are shown for both vision conditions (on/off) and both directions (ahead/side) at all ages (6/7/8 years). For medial-lateral error (c): negative values indicate left bias, positive values indicate right bias. For anterior-posterior error (d): negative values indicate backward bias, positive values indicate forward bias. Error bars show standard errors. Significant main effects are listed (with *p* values) at the top of each sub-plot where relevant.

In support of H1, absolute reach error was significantly greater with vision occluded (*M*=20.3mm, *SE*=2.4mm) than with vision available (*M*=9.1mm, *SE*=0.9mm) $F(1, 29)=34.375$, $p<.001$, $\eta p^2=0.542$ (Figure 2. 3a). Our predictions about age were not supported (H2). There was no effect of age or direction (*p*'s>.3) on absolute reach error. In support of H1, variable reach error was significantly greater with vision occluded (*M*=10.29mm, *SE*=0.65mm) than with vision available (*M*=7.6mm, *SE*=0.9mm) $F(1, 29)=9.115$, $p=.005$, $\eta p^2=0.239$ (Figure 2. 3b). However, contrary to H2, there was no effect of age on variable error (*p*=.359). There was no effect of direction on variable reach error (*p=.559*). There was no effect of vision, age or direction on constant reach error (*p's* >.06). Shoulder path length did not correlate with absolute reach error in any conditions (*p's*>.5).

We used a compromise power analysis in G*Power to assess the power of our analyses. We calculated implied power for detecting a large effect size (*f*=0.3), with an alpha level 0.05, and beta/alpha ratio=1. For stepping (children and adults): with a correlation among repeated measures of *r*=0.47 (calculated from our data), our sample of *N*=47 implies a power of 0.80 for between-subjects effects, 0.99 for within-subjects effects and 0.97 for interactions. For reaching (children only), with a correlation among repeated measures of r=0.70 (calculated from our data), our sample of N=32 implies a power of 0.72 for between-subjects effects, 0.995 for within-subjects effects and 0.99 for interactions.

2.4 Discussion

Adults rely on vision to guide steps, especially when walking in complex, natural environments (Matthis et al., 2018; Reynolds & Day, 2005a; Smid & Den Otter, 2013). Nonetheless, little research has addressed visually guided stepping developmentally. We show that children's precision stepping is visually guided (H1). However, unexpectedly (H2), we found the development of stepping was very different to reaching. Further, neither stepping nor reaching followed the non-linear developmental profile previously reported for reaching (Bard et al., 1990; Hay et al., 1991; Pellizzer & Hauert, 1996; Van Braeckel et al., 2007). We now elaborate on these findings as well as on the directional biases in step placement (H3) and the relationship between step error and postural stability (H4).

2.4.1 Children Show Adultlike Reliance on Vision for Precision Stepping

Children use online vision to control reaching (e.g. Bard et al., 1990; Chicoine et al., 1992). We show that children's precision stepping is also visually guided. Most interesting of all, we found that children aged 6, 7 and 8 years rely on vision for stepping to the same extent as adults. At 6 and 7 years, children's stepping error was overall higher than that for adults. However, the impact of visual occlusion on stepping error was equal at all ages. This suggests that children weight reliance on vision in an adultlike way. As hypothesised (H1), both steps and reaches were more accurate with vision available. Further, both reaches and steps straight ahead were more precise with vision available. We show that, like adults (Reynolds & Day, 2005a; Smid & Den Otter, 2013; Westwood et al., 2001), young children use online vision to fine-tune arm and leg movements and that stepping and reaching share similar visual control mechanism, likely controlled by parietal regions (Buneo & Andersen, 2006; Drew et al., 2008; Gwin et al., 2011)

Also, in support of our first hypothesis (H1), steps were more variable with vision occluded. Interestingly, this is qualified by an interaction with direction, such that it occurs only for straight-ahead steps. In fact, we had anticipated (H3) that side steps would be more challenging, since they deviate from the normal forward movement trajectory of walking. However, the higher error for straight steps may reflect their narrower, less stable base, which is more easily compromised when vision is removed.

Previous work has shown that children use vision during step descent (Cowie, Atkinson, et al., 2010), when walking in cluttered environments (Franchak & Adolph, 2010) and when approaching obstacles (Berard & Vallis, 2006). These complex and naturalistic tasks provide rich, ecological data.

However, they do not show whether children use online vision to fine-tune active steps – especially when the landing location is very small (a single target). In this study, we have shown that children do use online vision to carefully guide the foot to a constrained landing location. This behaviour is crucial when walking in complex environments, where only certain, small footholds afford stable forward progression.

2.4.2 Precision Stepping and Reaching Have Different Developmental Profiles

Based on the extensive literature on reaching (Bard et al., 1990; Hay et al., 1991; Pellizzer & Hauert, 1996; Van Braeckel et al., 2007), we anticipated a non-linear developmental profile for stepping (H2). In contrast, stepping error decreased gradually and linearly with age. By 8 years, both accuracy and variability for stepping were not significantly different to adult error. This compliments research showing adultlike step accuracy at 9 years during walking (Corporaal et al., 2018). Importantly, stepping error decreased with age both with and without vision. This suggests that development might be driven by improvements in proprioception, rather than by improvement in visual control.

In contrast, reaching error was stable between 6 and 8 years both with and without vision. We, therefore, show different developmental profiles for reaching and stepping and argue that both visually guided and non-visually guided action develop in a limb-specific manner. This supports independent assessment of upper (fine) and lower limb (gross) movement in developmental motor assessments (Cools et al., 2009). We should expect upper and lower limb visuomotor control to typically develop at different rates. Stepping continues maturing long after reaching – just like controlled stepping emerges later than reaching in infancy (Berger & Adolph, 2007). The neural control of precise movement of the arms and legs may be decoupled and develop asynchronously (Dietz, 2003).

We found no change in reaching error between 6 and 8 years. This contrasts with other studies. Numerous studies show a non-linear developmental trend (Bard et al., 1990; Hay, 1979; Hay et al., 1991; Pellizzer & Hauert, 1996; Van Braeckel et al., 2007). However, in previous work, reaches were much larger (Bard et al., 1990; Hay, 1979; Hay et al., 1991; Van Braeckel et al., 2007). In our task, children performed small reaches equally proficiently from 6- to 8-years, with reach error that was lower than i) step error and ii) reach error in previous studies (Bard et al, 1990). We argue that for our small reaches, children's performance was mature.

2.4.3 Does Postural Stability Constrain Precision Stepping Performance?

We predicted that biases in foot placement would widen and lengthen steps to increase stability (H3). However, our results only partially supported this. Steps were biased laterally (to the right) in the side condition. This bias widens the base of support. However, steps were also biased posteriorly in the side condition and medially in the ahead condition. Both of these biases narrow the base of support, arguably reducing stability. It is, therefore, possible that these biases are unrelated to stability and may be due to sensory or perceptual error.

Precision stepping requires children to guide the foot to a precise landing location, all whilst balancing on one leg. Since balance continues developing into adolescence (Godoi & Barela, 2008), we expected that balance would constrain children's stepping performance (H4). However, controlling for age, we found no correlation between postural stability and step error. We, therefore, argue that other factors – neural and cognitive development (Corporaal et al., 2018, 2017; Gogtay et al., 2004; Zelazo, 1983), motor imagery (Sooley, Cressman, & Martini, 2018), internal models (Contreras-Vidal, Bo, Boudreau, & Clark, 2005), and proprioception (King, Pangelinan, Kagerer, & Clark, 2010) – contribute to stepping development. Despite improvements in both postural stability and step error between 6 and 8 years, balance does not seem to be the most crucial factor in this simple, stepping task.

2.5 Conclusions

Children use online vision to fine-tune precise steps. We, therefore, show that precision stepping shares a visual control mechanism with other motor tasks, like reaching. However, precision stepping takes longer to mature. We argue that the earlier emergence of reaching relative to stepping provides earlier, more extensive opportunity for children to practice reaching. This leaves stepping (both visually guided and non-visually guided) maturing relatively later than reaching.

2.6 Limitations

Study 1 was published in *Experimental Brain Research* as presented above. However, we would now like to add some further discussion of the methodological limitations which were not present in this publication.

Firstly, we did not find a relationship between postural stability and stepping performance. Therefore, we argued that other factors (such as neural and cognitive development, motor imagery, internal models, and proprioception) are responsible for improvements in childhood stepping performance. However, it is counterintuitive that balance was not related to stepping performance given that to step precisely onto a target requires controlling the trajectory of one moving leg, whilst standing precariously on the other leg. Given that balance remains immature even in adolescence (Barozzi et al, 2014; Blaszczyk & Fredyk, 2021; Golomer et al, 1999) it would be very surprising if there really was no relationship between balance and precision stepping performance in younger children.

Using different measures of postural stability or balance might produce different results. In study 1, we measured postural stability during standing on two feet with and without vision. Even this very simple measure of postural stability showed significant change between 6 and 8 years (with postural stability still significantly poorer in 8 year olds compared to adults). However, this measure did not correlate with stepping performance. This could be because we measured postural stability in a stable, double-support posture, whereas stepping requires a child to temporarily balance on just one leg. Perhaps the balance demands of the two tasks are too far removed from one another. Future work should consider measuring static balance on one leg – since balancing on one leg is more closely aligned with the balance demands during stepping. An alternative approach would be to compare stepping performance with and without balance constraints. This could be achieved by asking children to make steps with and without a harness or support frame (to support balance), or whilst standing vs. sitting. It would also be prudent for future research to measure dynamic stability *during* the stepping action (e.g. by measuring changes in the centre of mass with additional motion capture markers on the body). Future research using a combination of these suggested approaches would help to clarify whether or not childhood improvements in precision stepping are in some way driven by improving balance.

Secondly, although our statistical analysis shows no significant difference in foot placement error between 8-year-olds and adults, there may still be further improvement between 8 years and adulthood. The data presented in Figure 2.2a and Figure 2.2b suggest that, although not statistically significant, mean foot placement error (both absolute and variable) is higher at 8-years than among adults. Since this is the first study to map the developmental profile of precision stepping in mid-childhood, future work should seek to replicate our design to give a clearer picture of the extent to which stepping performance really is adultlike (or not) at 8 years. Given that further replication work is needed, we must be cautious in our interpretation of study 1's findings. At 8 years, children's precision step performance was not significantly different to adults. However, it may not necessarily be fully mature. Nonetheless, we consider our finding that 6- to 8-year-olds use online vision to control precise stepping and reaching movements to be robust and a demonstration of sophisticated visual control.

2.7 From Single Steps to Complex Walking

Adult steps and reaches are visually guided (Babinsky et al., 2012; Berthier et al., 1996; Pisella et al., 2000; Reynolds & Day, 2005a; Reynolds & Day, 2005b; Smid & Den Otter, 2013; Westwood et al., 2001). In study 1, we asked whether children also use continuous, online visual input to fine-tune precise stepping and reaching movements. Six, 7, 8-year-olds, and adults made stepping and reaching movements toward a target. On some of the trials, we occluded vision at movement onset. We found that, like reaching, children's steps were visually guided to the same extent as adults'. Stepping error was higher with vision occluded and reduced with age until 8 years at which point stepping error was not significantly different to adult stepping error (although some further improvement beyond 8 years is likely; see section 2.6).

Given this, we wanted to extend our research to investigate whether 8-year-olds also show adultlike visual guidance during longer walking paths. To walk smoothly and safely around the environment, it is crucial to visually sample the upcoming terrain and adjust foot placement and walking speed appropriately. To achieve this, adults typically fixate upcoming footholds 2 steps in advance (Hollands et al., 1995; Patla & Vickers, 2003). They also walk more slowly (Matthis et al., 2017), show higher foot placement error (Matthis et al., 2015) and more frequent obstacle collisions (Matthis & Fajen, 2014; Matthis & Fajen, 2013) when visibility of the upcoming terrain is restricted to less than 2 step lengths ahead. In study 2, we wanted to establish whether children also show similar vision-action coupling during walking, and how these longer passages of control relate to single-step control. Would children plan ahead during walking like adults, or would they prefer to control walking one step at a time?

Chapter 3

Study 2 - Children's Walking in Complex Environments: One Step at a Time?

3.1 Introduction

The everyday environment is cluttered with obstacles, varying ground textures, slopes and drops. To walk safely and efficiently in such a complex environment, we rely on visual information to select appropriate footfalls. Failure to allocate visual attention effectively during walking is associated with slower walking and poorer step accuracy (Ellmers et al., 2016). Little research has investigated the influence of visual information on children's foot placement during complex walking, despite it being crucial for fluent movement. In this study, we investigate whether children adopt an adultlike strategy of feedforward visual sampling, or use an online visual strategy to guide walking one step at a time.

In this chapter, we draw a distinction between online control (using visual feedback to guide the current step into place) and feedforward control (using vision to plan the placement of a future step). However, even when using visual cues from a few steps ahead to pre-plan foot placement, vision is used continuously or 'online' for other purposes: to provide information about direction of travel, speed of movement, balance, and distance between the body and upcoming hazards, obstacles or targets (Gibson 1979; Marigold, 2008) Therefore, during walking there is no true dichotomy between online and feedforward control per se. However, although continuous visual input plays an important role during walking (in controlling heading, speed, balance, and obstacle/target detection) these aspects of visual control are not the focus of the current chapter. In this chapter, we define online control as using visual feedback to guide the current step. For example, when adults make single target-directed steps, online visual input from the foot and target is used to adjust the trajectory of the foot as it nears the ground for improved accuracy (Reynolds & Day, 2005a). Single step accuracy is poorer when vision is occluded at step onset, demonstrating that continuous online visual information is beneficial (Reynolds & Day, 2005a; Study 1). As we will discuss in the following introduction, adults typically do not control walking in this way. It would be energetically very costly to use vision in an online manner to carefully guide each individual step into place during walking. In the absence of a large developmental literature in this area, we examine whether children's walking also benefits from distal visual cues about the upcoming terrain (indicative of feedforward control); or whether children's walking behaviour is unaffected by distal visual cues (indicative of an online mode of control).

3.1.1 *Adult Visually Guided Walking – Feedforward and Flexible*

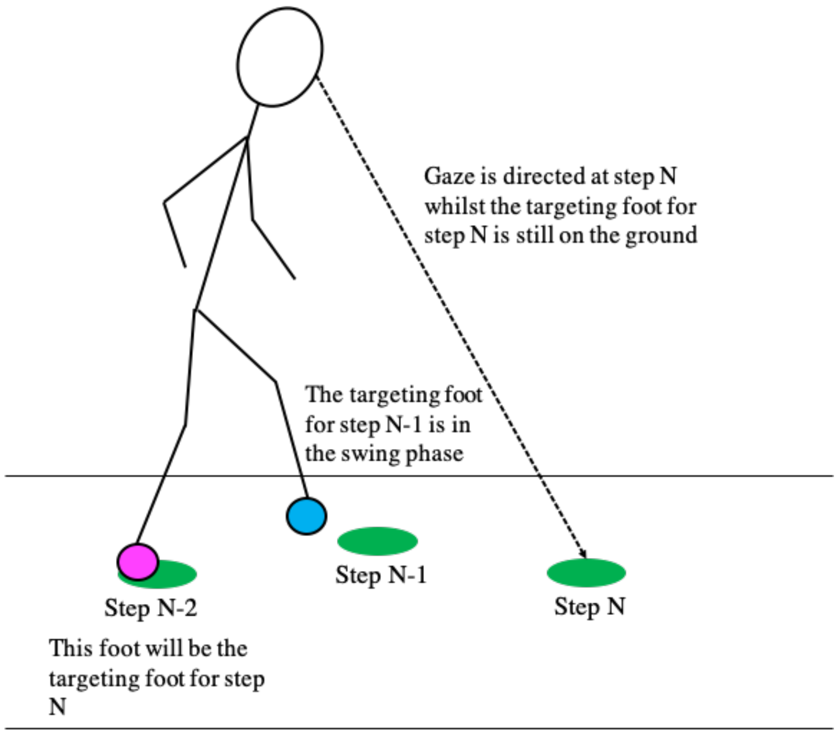

Figure 3. 1. Adult visually guided walking. Adults visually fixate from around 2 steps ahead during walking. Gaze is directed at step N, whilst the targeting foot for step N is still on the ground. The targeting foot is the foot which will be used to step onto a given target.

Researchers have studied adult visually guided walking by measuring gaze and foot placement as adults walk over a series of stepping targets. As illustrated in Figure 3. 1, adults tend to fixate the next target in a sequence whilst the targeting foot is still on the ground (Hollands et al., 1995). Adults visually sample from around 2 steps ahead, regardless of whether stepping targets are regularly or irregularly spaced (Patla & Vickers, 2003). Adults also walk more slowly when visual information is restricted. For example, if targets only become visible as the relevant foot enters the swing phase, compared to when targets become visible when the relevant foot is still on the floor (Matthis et al., 2017). Slowing down allows the relevant visual information to be sampled in sufficient time to respond to it (Hayhoe & Matthis, 2018). Given visual information from at least two steps ahead, adults also reduce the number of obstacle collisions in cluttered environments (Matthis & Fajen, 2014; Matthis & Fajen, 2013) and reduce foot placement error (Matthis et al., 2015). However, providing visual information from more than 2 steps ahead does not have additive benefits for foot placement error (Matthis & Fajen, 2014; Matthis & Fajen, 2013). When vision is occluded 2 steps ahead of a kerb descent, adults behave cautiously, leaving exaggerated margins of error between their foot and the kerb

(Buckley, Timmis, Scally, & Elliott, 2011). In sum, the preferred visual strategy of adults is to sample from 2 steps ahead.

These findings underpin the critical control phase hypothesis (Matthis et al., 2017). The critical control phase hypothesis states that i) a walker needs visual input from the foothold N, during step N-2, and ii) a walker no longer needs this visual input once the relevant foot for step N has entered the swing phase (Matthis et al., 2017). Once initiated, a step need not be actively guided into place. The walker can simply allow the foot to swing and fall passively, without muscular intervention. This is possible as long as the preceding step has been placed appropriately. By visually sampling from 2 step lengths ahead, the walker can place the foot in such a way that facilitates passive unfolding of subsequent steps (Matthis et al., 2017).

Although adults prefer to plan foot placement 2 steps ahead, in very complex environments there is a need for greater flexibility. When walking on very uneven natural terrain, adult gaze is more tightly coupled to upcoming footholds than when walking on flat terrain (Matthis et al., 2018). In medium-rough terrains, adults visually sample from 2 steps ahead, with gaze divided between 2 and 3 steps ahead in the roughest terrain (Matthis et al, 2018). However, adults do also occasionally look at the immediate terrain, just one step ahead, engaging in online, feedback driven control (Matthis et al, 2018). Due to the complex demands of the natural environment, adults flexibly employ a combination of feedforward planning and carefully controlled stepping, guided by online vision (Matthis et al., 2018).

Adults also adapt their visual strategies when walking under conditions of postural threat: conditions in which there is a heightened fear of falling. When walking on a raised walkway, adults show an increased tendency to look at the immediate walkway, at the expense of visually sampling upcoming step targets (Ellmers & Young, 2019). Similar behaviour is seen in older adults at high risk of falling, even when walking on a flat terrain (Ellmers, Cocks, & Young, 2019). In summary, although the preferred mode of control is to visually sample from 2 steps ahead, adult behaviour can change depending on the complexity of the terrain and the postural threat level.

3.1.2 A One Step at a Time Strategy for Children?

What kind of strategy might children use to control their walking? There is some evidence that children use online vision to control and fine-tune individual steps. For example, without vision, children are less able to tailor leg trajectory to step height when stepping down (Cowie, Atkinson, et al., 2010). Between 6 and 8 years, children also show poorer accuracy for single steps on flat ground when vision is occluded (Mowbray, Gottwald, Zhao, Atkinson, & Cowie, 2019; Study 1). Therefore, even young children do rely on online vision to carefully guide precise, single steps like adults

(Reynolds & Day, 2005a). Given this, one hypothesis might be that children also control walking in an online manner, visually guiding each individual step into place. Since children seem to rely on online vision to control single steps (Cowie, Atkinson, et al., 2010; Mowbray et al., 2019; Study 1), they may struggle to engage in a more mature feedforward mode of control. A one step at a time strategy might be beneficial for children, since it reduces the need for complex, feedforward plans which could be very cognitively demanding. However, a one step at a time approach would be very energetically demanding. It would disrupt the ballistic, pendulum-like walking motion (Matthis et al., 2017). It would also mean accommodating obstacles or changes in the environment at the last minute. This would involve rapid online adjustments that could threaten postural stability.

3.1.3 A Feedforward Strategy for Children?

Given how inefficient and effortful a one step at a time strategy would be, it seems more likely that children might control walking in a more adultlike feedforward manner. There is evidence that children can plan walking in advance from an early age. For example, toddlers slow down when approaching obstacles (Mulvey, Ulrich, Masayoshi, & Chang, 2011) and 3- to 5-year-olds adjust foot placement up to 4 steps in advance of obstacle crossing (Mowbray & Cowie, 2020). There is some eye tracking evidence that, by 4 years, children fixate obstacles a few steps in advance of obstacle encounters (Franchak & Adolph, 2010). At 7 years, children reduce walking speed for upcoming obstacle crossing in low-light conditions (Berard & Vallis, 2006). These examples suggest that children can use distal visual cues to plan and adjust their walking in a feedforward manner when approaching obstacles.

Obstacle crossing is an avoidance task. The feet can be placed flexibly, providing they do not collide with the obstacle. What about children's ability to step accurately onto specific locations, as when walking a rocky path or in a messy room? The feet must be placed into specific, tightly constrained footholds to facilitate smooth forward progression. The above-mentioned obstacle-crossing studies do not speak to this type of task. Very little work has used a target-stepping paradigm to study visually guided walking in children. Corporaal et al (2018) used step targets presented on a treadmill and found adultlike accuracy in precision stepping by around 8 years, with variability of foot placement reducing through adolescence (Corporaal et al., 2018). However, without manipulating the visibility of upcoming step targets, we cannot tell whether these children were visually sampling from ahead, or whether they were adopting a one step at a time strategy. Further, the treadmill paradigm did not permit spontaneous adjustments to walking speed. Speed adjustments can be an interesting indicator of visually guided control.

3.1.4 The Present Studies

We conducted two studies to understand children's visually guided walking, in order to establish whether children would plan ahead like adults, or whether they would control walking one step at a time. In study 2.1, we manipulated the number of visible upcoming stepping targets. In study 2.2, we additionally manipulated the level of threat, comparing walking on a flat surface (low threat) vs. walking on raised stepping targets (high threat).

3.1.4.1 Study 2. 1. In immersive VR, 30 adults and 30 8-year-olds walked across a series of raised stepping targets. The number of visible upcoming targets varied between 1 and 3, with the next target in the sequence appearing with each new step. We recorded foot placement error and time to complete each trial using Vicon Tracker software. Participants also completed a single step task in which we manipulated the visibility of the step target. We included this single step task to assess participants' ability to make simple, visually guided movements in the novel VR environment.

For the walking task, we made the following hypotheses: H1 - adults and children will plan ahead to reduce foot placement error, such that error will be lower given 2 or 3 visible upcoming targets (as per adults in Matthis et al., 2015, 2017). H2 - adults and children will adjust walking speed appropriately: they will take longer to complete each trial given only 1 visible upcoming target (Matthis & Fajen, 2014; Matthis & Fajen, 2013). H3 - children's performance will be partially adultlike: their foot placement accuracy will be adultlike, whilst their foot placement variability will be higher than adults' (as per Corporaal et al., 2018). For the stepping task, we made the following hypothesis: H4 - children's single step error will not be significantly different to adults' (as per children in Mowbray et al., 2019).

3.2 Methods – Study 2.1

3.2.1 Participants

Using G*Power software (Faul, Erdfelder, Lang, & Buchner, 2007), we conducted an a priori power analysis to determine the required sample size. Previous work by Matthis et al (2015) found a large effect size for the manipulation of target visibility on foot placement error (η^2=0.76). However, we did not have data from a comparable task with children. Therefore, we used a more conservative medium effect size (f=0.3) in our power analyses. We entered the following parameters: alpha=0.05, number of groups=2 (adult, child), number of measures=6 (vision, 3 levels x foot, 2 levels), non-sphericity correction=1, and a conservative estimate of 0.1 for the correlation between repeated measures. Given these parameters, to obtain power of 0.8 in our 2 (age) x 2 (foot) x 3 (visibility) design required a total sample of 24 participants for within subjects effects, between subjects effects and for interactions.

We also wanted to conduct an exploratory ANCOVA analysis with static balance (standing on one leg) and dynamic balance (heel to toe walking along a line) as covariates. We used a compromise power analysis with the following parameters: effect size f=0.3, beta/alpha ratio=0.5, total sample size=50, numerator df=2, number of groups=2, covariates=2. Given these parameters, a sample size of 50 would give a power of 0.83. We decided on a sample of 60 participants to increase our power.

Thirty children (10 female; mean age =7.95 years, *SE*=0.06 years; mean leg length = 65.77cm, *SE*=0.78cm) and 30 adults (23 female; mean age = 24.22 years, *SE*= 1.25 years; mean leg length = 90.23cm, *SE*=1.02cm) participated. Children were recruited via the Durham Developmental Group Families Database and adults were recruited via opportunity sampling and via the Durham Psychology Department Participant Pool. Participants did not have any previous reported neurological or muscular deficits, developmental or coordination disorders, lower limb physical disabilities, epilepsy or significant visual impairments. Participants and parents provided written informed consent and all procedures were in accordance with the ethical standards of the Durham University Ethics Committee.

3.2.2 Design

All participants completed a static and a dynamic balance task (order counterbalanced). All participants then completed a walking task and a stepping task in VR (order counterbalanced). The walking task included 30 trials with the following within-subjects variables: visibility (3 levels: 1 step ahead, 2 steps ahead, 3 steps ahead) and foot (2 levels: dominant, non-dominant). The number of visible targets on each trial was randomised. We recorded foot placement error on each stepping target. In the stepping task, there were 20 trials with 2 within-subjects variables: foot (2 levels: dominant, non-dominant) and vision (2 levels: available, occluded). We randomised the visual conditions and the foot used across trials.

3.2.3 Experimental Set-Up

The static balance test used a balance board from the Movement Assessment Battery for Children 2 (Henderson, Sugden & Barnett, 2007). The dynamic balance test used a straight line marked onto the floor with masking tape. For the walking and stepping tasks, participants wore motion capture marker clusters (rigid bodies) on their feet, attached using Velcro straps. There were also motion capture markers attached to the Oculus Rift VR headset. We tracked participants' movements using 16 infrared Vicon cameras and Vicon Tracker software. Motion information was fed from Vicon Tracker into Vizard VR software. Vizard generates a virtual world in which distances and movements share a 1:1

scale with the real world and real movements. Vizard has been used in many previous academic psychology research studies, in military training, and in healthcare settings (full documentation available at worldviz.com/vizard-virtual-reality-software).

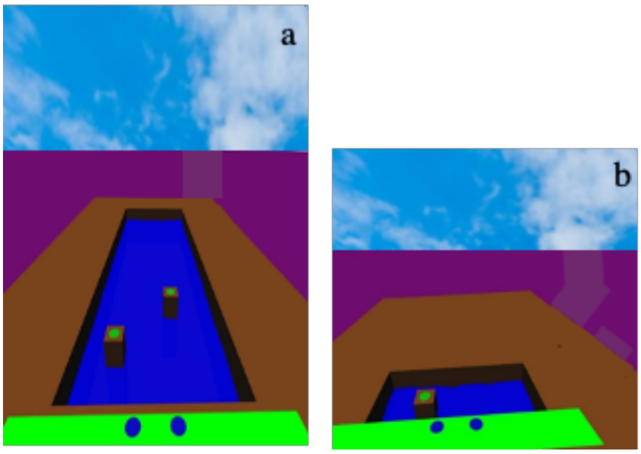

Figure 3. 2. Study 2.1. virtual reality tasks for walking (a) and stepping (b).

3.2.3.1 The Walking Task (Figure 3.2a). In VR, the feet were represented by coloured spheres (radius=5cm). The left foot was blue, the right foot was pink. A rectangular start area (width=2 x leg length, length=0.3 x leg length) was located at one end of a rectangular pool of water (width=1.5 x leg length, length=4.5 x leg length). On the start area, there were two circular starting positions for the virtual feet (radius=5cm).

In the 1 step ahead condition, just one stepping stone was visible at the start of each trial. In the 2 steps ahead condition, 2 were visible; in the 3 steps ahead condition, 3 were visible. Each stepping stone was a brown square (width=17cm, length=17cm) with a green target circle (radius=5cm) in the centre. The first stepping stone appeared alternately to the left or right of centre. In all conditions, once the participant stepped onto the first stone, a further stone appeared in the path. With each new step, another stone appeared. The stones were equally spaced in the anterior-posterior axis and the medial-lateral position of stones for the right foot was jittered (Figure 3. 3). This jitter was important since both adults and children can learn target stepping sequences (Choi, Jensen, & Nielsen, 2016) and we did not wish to test sequence learning in this experiment. Erroneously, the stepping target location for the left foot remained constant and we might therefore expect to find less error in the left foot data.

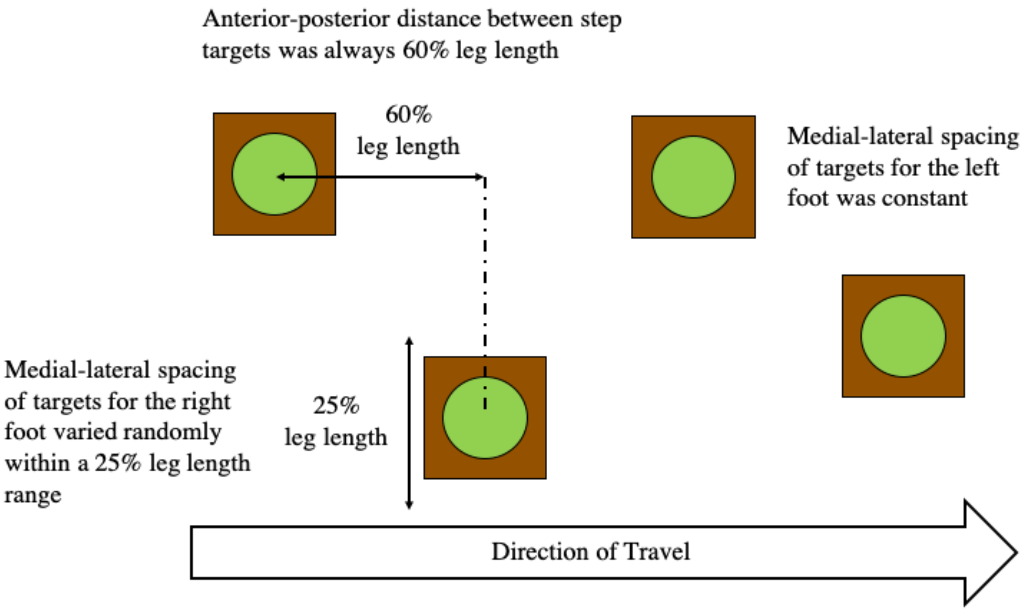

Figure 3. 3. Study 2.1 walking task target spacing.

To trigger stones appearing, a step was defined as when the virtual foot met all three of the following criteria: (i) foot position is within the area of a stepping stone in the ground plane (ii), foot is not moving (iii), foot vertical position < 10cm above floor. Once the participant had walked over all 7 stepping stones, the start area turned red in preparation for the next trial.

During walks, we recorded the time at which the foot landed on each stepping target as well as foot placement error for each stepping target. Error was the distance between the centre of the virtual foot and the centre of the stepping target. Up to 3 gold coins appeared at the end of the pool to reward accurate foot placement. Coins were allocated based on the cumulative absolute error across the 7 steps of the trial: error < 30cm=3 gold coins, error > 30cm < 50cm=2 gold coins and error > 50cmm=1 gold coin. After the 7th step on each trial, large red arrows appeared both at the end of the pool and on the left had side of the pool, directing the participant to walk back to the start position.

3.2.3.2 The Stepping Task (Figure 3.2b). In the single step task, the start area was identical to that in the walking task. The pool was 1.5 x leg length wide and 0.7 x leg length long. The start of each trial was triggered by an experimenter mouse click, which caused the start area to turn green. Only one stepping stone was present on any one trial (same size as those in the walking task). The stepping stone was located either to the left or right of centre, anterior posterior position of the stones was constant. The medial-lateral placement of each stepping stone (on both sides) was jittered within a 10% leg length range.

A step was defined as per the walking task and error was also calculated in the same way. After each step, gold coins appeared in front of the pool. Coins were allocated using the following criteria: error < 2cm=3 gold coins, error > 2cm < 4cm=2 gold coins and error > 4cm=1 gold coin.

3.2.4 Procedure

Adult participants and parents provided written informed consent. Children provided verbal assent. We measured participant leg length from anterior superior iliac spine (pelvis) to medial malleolus (inner ankle). We asked participants if they were right or left handed (which hand they write with) and whether they were left or right footed (which foot they would preferentially kick a ball with). To assess static balance, we recorded how long participants could stand on one leg on the balance board for (up to one minute). To assess dynamic balance, participants walked heel-to-toe along a straight line marked on the floor. Participants walked for 20 steps along the line and the experimenter noted how many steps the participant completed without stepping off the line or leaving a gap between the heel and toe. For both balance tasks, participants had two attempts starting with/standing on the left and right foot and an average score was calculated across the four attempts. The order of the static and dynamic balance tasks was counterbalanced across participants. Next, participants completed the stepping and walking tasks (order counterbalanced).

3.2.4.1 The Stepping Task. The experimenter explained that on each trial there would be one stepping stone visible and that the participant should make one step, placing their foot as accurately as possible into the centre of the green target. The participant was also told that they would earn gold coins (up to three per trial) for accuracy. The experimenter explained that sometimes the stepping stone would disappear during their step, but that they should continue with their step and would receive feedback (gold coins) on step completion.

To begin, participants stood with their feet on the start positions, facing a small pool of water. At the start of each trial, the experimenter clicked the mouse to turn the start area green. Each trial required a single step using the left or right foot (randomised across trials). On each trial, one of the virtual feet disappeared and a stepping stone appeared in front of the remaining virtual foot. The experimenter verbally instructed the participant to use the 'pink' or 'blue' foot and the participant made their step. On half of trials, the stepping stone and virtual foot were made invisible as the foot left the floor (when the foot's vertical position was >10cm above the floor). The foot and stepping stone reappeared once the participant landed their step. Up to three gold coins were displayed to reward accuracy. The participant then returned their foot to the start position.

On the rare occasion that a participant made a very inaccurate step (which fell outside of the stepping stone surrounding the green target), the next trial could not be triggered. In this scenario, the participant was asked to return their foot to the start position and step again to complete the trial. Before completing the 20 recorded trials, participants were allowed to practice the task to get used to the task and the control of the virtual feet. The experimenter allowed the participant to practice the task until they were able to make singular, defined stepping movements that did not involve sliding the foot along the ground or shuffling the foot toward the target.

3.2.4.2 The Walking Task. The experimenter explained that the aim was to walk over the stepping stone targets placing the virtual feet as accurately as possible into the centre of the green targets. The participant was also told that they would earn up to three gold coins per trial for accuracy. The experimenter explained that the participant might not be able to see many stepping stones to begin with, but that these would pop up as they walked along. To begin, participants stood with both virtual feet on the start positions facing the pool of water. At the start of each trial, the experimenter clicked the mouse, turning the start area green. The experimenter verbally instructed the participant to start walking with their 'pink' or 'blue' foot. The participant then began walking over the 7 stepping stones. At the end of the pool, the participant stepped onto the brown surrounding area and gold coins appeared to reward accuracy. The participant then walked back around the side of the pool back to the start position, following the red arrows for guidance.

If a participant failed to step onto any one of the stepping stones, then the upcoming stones would not appear. If this happened, the participant was asked to start the trial again and the trial was not included in the analysis (because time was a dependent variable). On the rare occasion that a participant fell, the trial was also excluded from the analysis. As per the stepping task, participants were allowed to practice the walking task before the 30 recorded trials. Participants practiced until they were able to walk across the stepping stones without shuffling their feet along the floor and without falling.

3.2.5 Analysis

We used mixed model ANOVAs to analyse our data. For the walking task: visibility (1, 2, 3 steps ahead) x foot (dominant, non-dominant) x age (adult, child). For the stepping task: foot (dominant, non-dominant) x vision (available, occluded) x age (adult, child). Significant interactions were further analysed using Bonferroni-corrected post-hoc tests. We applied a Greenhouse-Geisser correction where the sphericity assumption was not met. Error values are given in centimetres. Time values are given in seconds. We used an ANCOVA analysis to look for effects of static and dynamic balance (the covariates) on foot placement error as an additional exploratory analysis.

3.3 Results – Study 2.1

3.3.1 H1 (Walking) – Foot placement error will be lower given 2 or 3 visible upcoming targets.

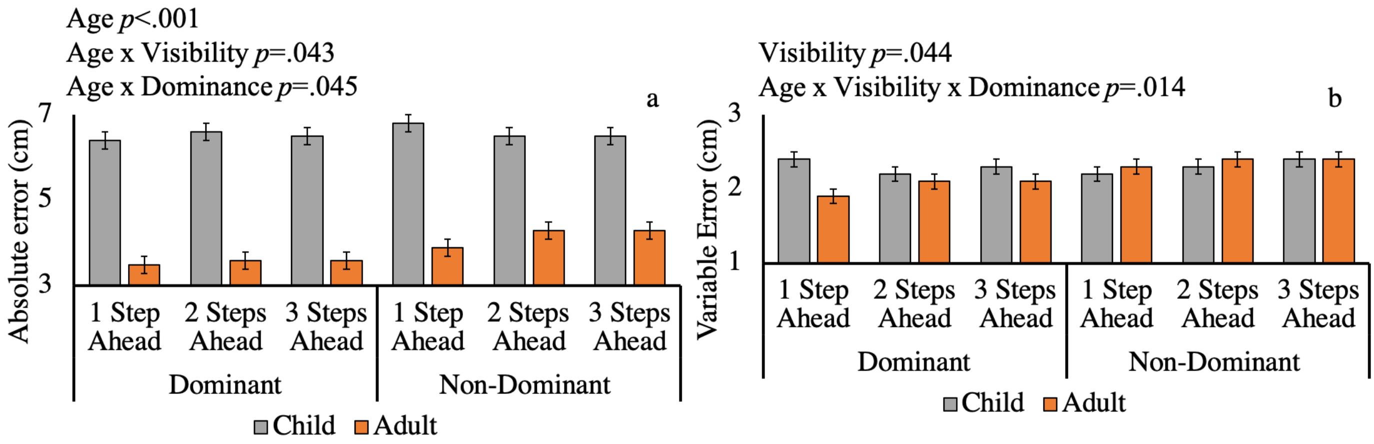

Figure 3. 4. Study 2.1 mean foot placement error (cm) for children and adults, given for both feet and in each of the visibility conditions of the walking task - absolute error (a), variable error (b). Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant main effects and interactions are listed (with *p* values) at the top of each sub-plot.

H1 was not supported. We found no significant effect of visibility on absolute error (Figure 3.4a; p=.094). However, there was a significant interaction between age and visibility on absolute error $F(2, 116)=3.234$, p=.043, ηp^2=0.053 (Figure 3.4a). For adults, there was a significant effect of visibility $F(2, 29)=5.100$, p=.009, ηp^2=0.15 (Figure 3.4a). Adults' absolute error was significantly higher in the 3 steps ahead condition (M=4.0cm, SE=0.2cm) than the 1 step ahead condition (M=3.7cm, SE=0.2m) p=.027. Other post hoc comparisons were non-significant p's>.05. However, for children, there was no significant effect of visibility on absolute error p=.552.

In contrast, there was a significant main effect of visibility on variable error $F(2, 116)=3.198$, p=.044, ηp^2=0.052 (Figure 3.4b). However, this effect was small and not in the direction we expected. Variable error in the 1 step ahead condition (M=2.2cm, SE=0.10cm) was significantly lower than in the 3 steps ahead condition (M=2.3cm, SE=0.10cm) p=.049. All other post-hoc comparisons were non-significant p's > .50.

3.3.2 H2 (Walking) - Time taken to complete each trial will be higher given just 1 visible upcoming target

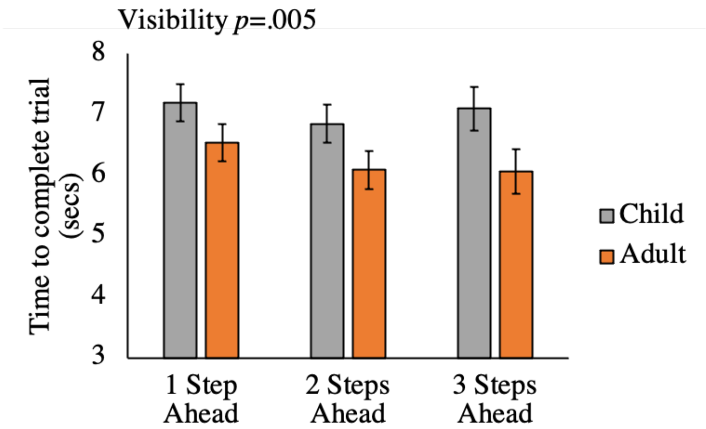

Figure 3. 5. Study 2.1 mean time to complete each trial (secs) in each of the visibility conditions of the walking task for adults and children. Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant main effect of visibility (with *p* value) is given at the top of the figure.

As predicted (H2), there was a main effect of visibility on time $F(2, 116)=6.172$, $p=.005$, $\eta p^2=0.096$ (Figure 3. 5). Participants took longer to complete each trial in the 1 step ahead condition (M=6.9 secs, SE=0.2 secs) than in the 2 steps ahead condition (M=6.5 secs, SE=0.2 secs) $p<.001$. All other post hoc comparisons were non-significant, p's>.08.

3.3.3 H3 (Walking) - Children's absolute error will be adultlike, whilst their variable error will be higher than adults'

Contrary to H3, children's absolute error (M=6.6cm, SE=0.2cm) was significantly higher than adults' (M=3.9cm, SE=0.2cm) $F(1, 58)=135.202$, $p<.001$, $\eta p^2=0.70$ (Figure 3.4a). Also contrary to H3, we found no significant effect of age on variable error ($p=.387$).

3.3.4 H4 (Stepping) - Children's single step error will not be significantly different to adults'

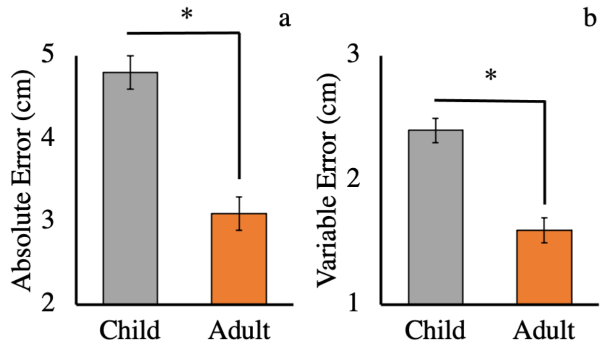

Figure 3. 6. Study 2.1 mean foot placement error (cm) for children and adults on the stepping task - absolute error (a), variable error (b). Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant differences between children and adults are indicated by asterisks.

Contrary to H4, children's absolute error (*M*=4.8cm, *SE*=0.2cm) was significantly higher than adults' (*M*=3.1cm, *SE*=0.2cm) on the stepping task $F(1, 58)=23.049$, $p<.001$, $\eta p^2=0.284$ (Figure 3. 6a). Children's variable error (*M*=2.4cm, *SE*=0.1) was also significantly higher than adults' (*M*=1.6cm, *SE*=0.1) on the stepping task $F(1, 58)=25.082$, $p<.001$, $\eta p^2=0.302$ (Figure 3. 6b).

3.3.5 Additional Findings – Study 2.1.

Children had significantly poorer static balance (*M*=14.99 secs, *SE*=2.10 secs) than adults (*M*=29.61 secs, *SE*=3.53 secs) $t(58)=3.573$, $p=.001$ and significantly poorer dynamic balance (*M*=14.5 steps, *SE*=1.0 steps) than adults (*M*=19.3 steps, *SE*=0.3 steps) $t(58)=4.89$, $p<.001$. To establish whether balance had an impact on stepping error, we calculated partial correlations, controlling for age. There were no significant correlations between dynamic or static balance and absolute stepping error in any of the conditions for the single step task *p*'s>.1. For the walking task, we included balance as a covariate (ANCOVA) and found no significant effect of static or dynamic balance on absolute stepping error *p*'s>.4.

For absolute error (walking task), there was also a significant interaction between age and foot dominance $F(1, 58)=4.189$, $p=.045$, $\eta p^2=0.067$ (Figure 3.4a). Adults also showed a significant effect of foot $F(1, 29)=14.087$, $p=.001$, $\eta p^2=0.327$. Adults' absolute error was significantly higher for the non-dominant foot (*M*=4.2cm, *SE*=0.2cm) compared to the dominant foot (*M*=3.6cm, *SE*=0.2cm). For children, there was an interaction between visibility and foot $F(2, 58)=3.676$, $p=.031$, $\eta p^2=0.113$. However, no post-hoc comparisons were significant *p*'s>.1.

For variable error (walking task), there was a significant 3 way interaction between age, visibility and foot dominance $F(2, 116)=4.402$, $p=.014$, $\eta p^2=0.071$ (Figure 3.4b). For adults there was a significant effect of visibility $F(2, 29)=3.823$, $p=.028$, $\eta p^2=0.116$. Adults' variable error was significantly higher in the 3 steps ahead condition (M=2.2cm, SE=0.1cm) than in the 1 step ahead condition (M=2.1cm, SE=0.1cm) $p=.049$. Other post hoc comparisons were non-significant p's>.1. Adults also showed a significant effect of foot $F(1, 29)=14.707$, $p=.001$, $\eta p^2=0.336$. Adults' variable error was significant higher for the non-dominant foot (M=2.3cm, SE=0.1cm) compared to the dominant foot (M=2.0cm, SE=0.1cm). For children, there was a significant interaction between visibility and foot $F(2, 58)=5.050$, $p=.01$, $\eta p^2=0.148$. However, the only significant post hoc comparison was for the non-dominant foot, error was higher in the 3 steps ahead condition (M=2.4cm, SE=0.1cm) than in the 1 step ahead condition (M=2.2cm, SE=0.1cm) $p=.017$. All other post hoc tests were non-significant p's>.1.

Finally, for the walking task we conducted Pearson's correlations to see if adults' absolute error (averaged across both the dominant and dominant foot) correlated significantly with time to complete trial. We would expect this since adults reduced both speed and foot placement error when visual information was restricted to just 1 step ahead. However, there was no significant correlation between absolute error and time taken to complete the trial in any of the visibility conditions (p's>.1).

3.3.6 Results Summary and Discussion – Study 2.1

Based on the findings of Matthis and colleagues, we expected that adults and children would show lower foot placement error given visual information from at least 2 steps ahead (H1). We also expected them to walk more quickly given visual information from at least 2 steps ahead (H2). Our findings supported H2, but not H1. When visual information was available from 2 steps ahead, both children and adults completed trials more quickly compared to the 1 step ahead visibility condition. However, for adults, greater visibility was also associated with higher foot placement error. Children's foot placement was overall less accurate than adults', both during walking and for single steps. This was contrary to our prediction that by 8 years children's foot placement accuracy would be adultlike during both stepping and walking (H3, H4).

Our findings partially align with those of Matthis and colleagues. Like Matthis and Fajen (2013, 2014), we found that given visual information from at least 2 steps ahead, both children and adults completed trials more quickly. However, in direct contrast to Matthis et al (2015, 2017), we found that when visual information was restricted to just 1 step ahead, foot placement error was lower for both children and adults. We interpret this as participants exercising greater caution (by slowing down and placing feet more carefully) when they cannot plan at least 2 steps ahead.

But why might our result contrast with those of Matthis and colleagues? Firstly, in study 2.1. we encouraged accurate foot placement by rewarding accuracy with virtual gold coins (especially because we were working with children). However, rewards of this type are clearly not a feature of natural walking and were not implemented in any work by Matthis and colleagues. Secondly, unlike the work of Matthis and colleagues, our paradigm is virtual-reality based. It is possible that the virtual environment was challenging for both adults and children (for example there are fewer depth cues available in VR and the only visible body parts were virtual feet). A third possibility is that our paradigm (walking over raised stepping stones) evoked feelings of postural threat. Such threat may not have been present in the paradigms used by Matthis and colleagues which required participants to walk on flat ground.

To address these issues, we updated our methods for study 2.2. In study 2.2, we removed the gold coin rewards, added additional depth cues to the virtual environment, and provided longer and more standardised practice within the virtual environment. We also directly compared high threat (raised stepping targets as per study 2.1) and low threat (flat stepping targets) conditions. Matthis et al (2015, 2017) did also impose restrictions on walking speed, such that participants had 5 seconds to complete each trial. We did not wish to do this since we were interested in measuring natural adjustments to walking speed. Nonetheless, this methodological difference might contribute to the difference in findings, since our participants were allowed to complete trials more slowly than those of Matthis and colleagues.

3.4 Study 2.2

In study 2.2, we made some changes to improve the validity of our methods and to answer additional questions about visually guided walking in different environments. We will now discuss the main changes in three areas: rewards, the VR experience, and postural threat.

Firstly, we changed the way that participants were rewarded for task performance. In study 2.1, participants were explicitly rewarded with virtual gold coins if they performed the task accurately. We did this to ensure that participants were motivated to step accurately. However, in study 2.2, we decided that these explicit rewards were unnecessary, since accurate foot placement and successful walking are intrinsically rewarding, especially when accuracy is a task requirement (we explicitly asked participants to step as accurately as possible). Previous research has shown that when participants are instructed to place their feet as accurately as possible onto the centre of targets, their foot placement is significantly lower than when they are instructed to step onto targets with no particular requirement to step in the target centres (Domínguez-Zamora, Gunn, & Marigold, 2018). Therefore, our instructions to participants were sufficient to encourage accurate foot placement, without introducing additional, explicit rewards.

Secondly, we made changes to the virtual environment and the experience participants had in the environment to make sure that the VR experience was as comfortable and familiar as possible. The size of our own body parts are an important cue for understanding the spatial layout of the environment (Linkenauger, Leyrer, Bülthoff, & Mohler, 2013). A particular challenge in our virtual environment is that the participant's own body is not visible (they have just virtual feet represented by coloured spheres). Without familiar body or environmental cues, it may be difficult for participants to interpret the size of objects (e.g. the virtual stepping stones) as well as depth and distance (e.g. the distance between stepping stones).To mitigate this, we added some familiar objects to the virtual environment (a tree, skateboard, ball and bucket) to act as size and depth cues (Wann & Mon-Williams, 1996). We also standardised the amount of practice that participants had of moving in the virtual environment before beginning the trials. The amount of experience individuals have of moving in VR has an impact on their ability to perceive distances in VR relative to the virtual body (Linkenauger, Bülthoff, & Mohler, 2015). Therefore, it was important that all participants were equally experienced in moving the virtual feet.

Thirdly, we investigated postural threat. Postural threat (environmental conditions which evoke a fear of falling) has an impact on visually guided walking behaviour in adults. Researchers have evoked a feeling of postural threat by having participants walk on an elevated pathway. In this scenario, adults show an increased tendency to look at the immediate walkway, at the expense of visually sampling upcoming step targets (Ellmers & Young, 2019**.** In older adults, walking on an elevated platform is associated with more cautious behaviour, such as choosing to descend a step toe-first as opposed to heel-first (Kluft et al., 2020). In study 2.1, we also observed cautious behaviour which could have been triggered by postural threat associated with walking on raised stepping stones. In study 2.2, we further investigated postural threat in adults and children by directly comparing visually guided walking in high and low postural threat environments.

In summary, study 2.2 sought to more closely approximate natural walking behaviour by removing artificial rewards for accuracy and by using extra practice and depth cues to help participants adapt to the VR environment. With these improvements, we also manipulated postural threat.

Study 2.2 included the same walking task and single step task as study 2.1. Different to study 2.1, participants completed the task walking both on a flat surface (low threat), and on raised stepping targets (high threat). We made the following hypotheses for the walking task: H1 - threat and visibility will interact: in the flat (low threat) condition, we expected that error would be higher when vision is restricted to just 1 step ahead (as per Matthis et al., 2015, 2017). In the raised (high threat) condition, we expected that error would be lower when vision is restricted to just 1 step ahead, as per study 2.1. H2 - adults and children will take less time to complete each trial given greater visibility, regardless of the threat level, as per study 2.1 and per Matthis and Fajen (2013, 2014). H3 - children's foot placement error during walking will be higher than adults', as per study 2.1. H4 - foot placement error during walking will be lower in the raised condition for adults, since adults in study 2.1 behaved cautiously and reduced error in more challenging conditions.

We made the following hypotheses for the stepping task: H5a - error will be higher for children than adults (as per study 2.1). H5b – error will be higher in the flat condition than the raised condition. This is because in study 2.1 participants behaved cautiously in more challenging conditions. For adults, this involved more careful foot placement. Children did not adjust foot placement accuracy during walking in study 2.1. However, we expect that children would achieve such adjustments during the simpler, single step task in response to more challenging conditions (such as the raised condition).

3.5 Methods - Study 2.2

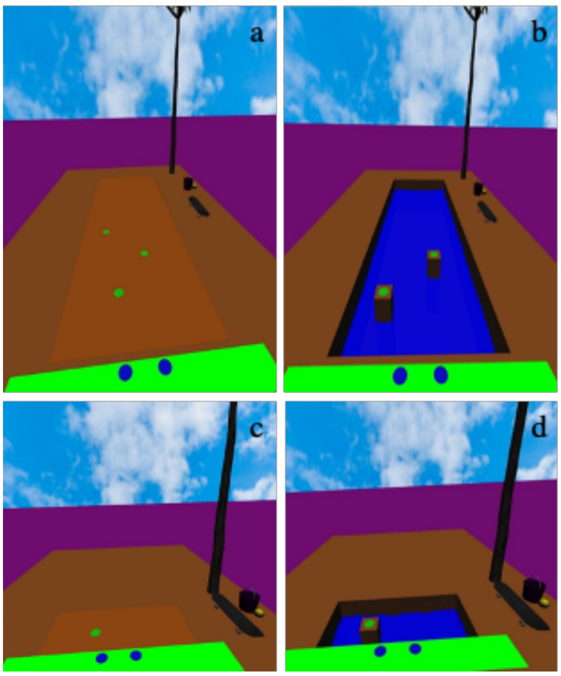

Figure 3. 7. Study 2.2 virtual reality tasks for walking on flat - low threat (a) and raised – high threat (b) terrain and stepping on flat – low threat (c) and raised – high threat (d) terrain.

The set-up and procedures used in study 2.2 were largely the same as study 2.1 and participants were given the same instructions. Here, we will outline the key differences. In study 2.2, participants did not receive any gold coins – they did not receive any feedback at all on their accuracy. We decided to take this approach so that we could examine natural behaviour as far as possible. To aid with depth perception, we added some familiar virtual objects to the VR environment at the side of the walkway (tree, skateboard, bucket, and tennis ball; Figure 3.7). Participants completed both the walking and stepping task on raised stepping targets (high threat), and on a flat surface (low threat; Figure 3.7). In the flat surface condition, the stepping targets appeared flush to the ground, such that only the green target circles were visible. In study 2.2 we also formalised our procedures for task practice. Each participant was given 10 practice trials on the stepping task and 4 practice trials on the walking task, before completing any recorded trials. Finally, the position of both the left and right foot was jittered in the medial-lateral axis (this corrected the minor error in study 2.1) as shown in Figure 3. 8. The order in which participants completed the stepping and walking task, and the flat and raised conditions was counterbalanced.

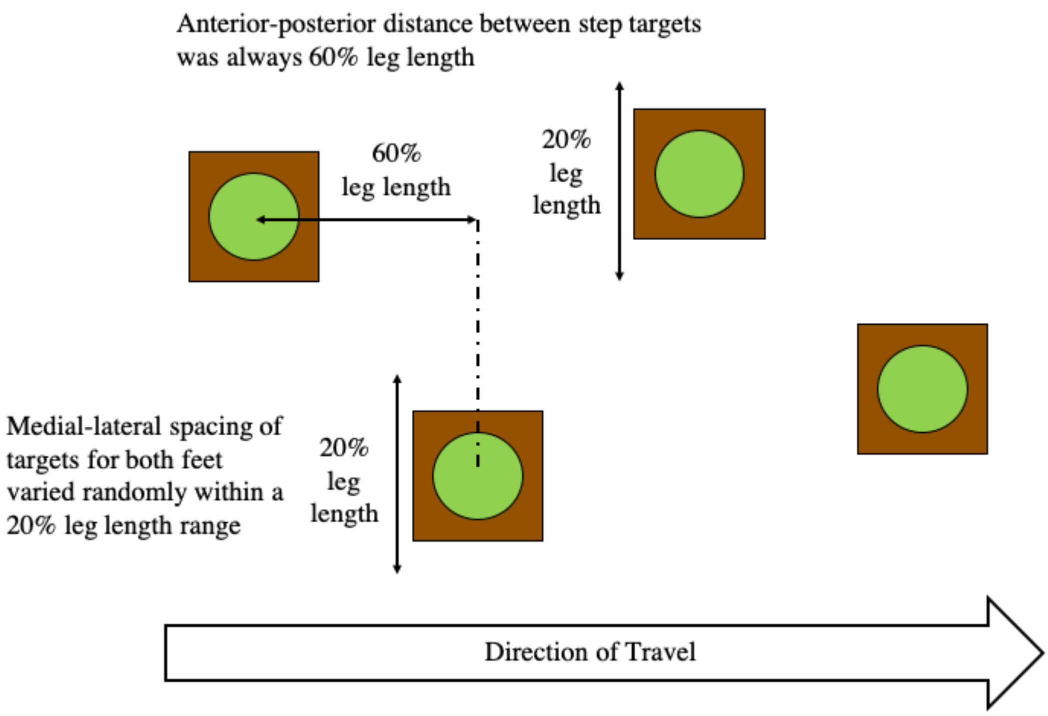

Figure 3. 8. Study 2.2 walking task target spacing.

3.5.1 Participants

To match the sample size of study 2.1 we aimed for a sample of 60 (30 adults, 30 children). However, due to the coronavirus pandemic, we were unable to finish collecting data from children. Therefore, in study 2.2, we had a sample of 16 children (6 female; mean age =7.88 years, *SE*=0.07

years; mean leg length = 68.44cm, *SE*=0.13cm) and 30 adults (11 female; mean age = 20.90 years, *SE*= 0.09 years; mean leg length = 93.13cm, *SE*=1.25cm). Children were recruited via the Durham Developmental Group Families Database and adults were recruited via opportunity sampling and via the Durham Psychology Department Participant Pool. Participants did not have any previous reported neurological or muscular deficits, developmental or coordination disorders, lower limb physical disabilities, epilepsy or significant visual impairments. Participants and parents provided written informed consent and all procedures were in accordance with the ethical standards of the Durham University Ethics Committee.

3.5.2 Design

All participants completed a static and a dynamic balance task (order counterbalanced). All participants then completed two walking tasks (flat and raised) and two stepping tasks (flat and raised) in VR. Half of the participants completed the walking tasks first, and half completed the stepping tasks first. The order of the threat conditions was counterbalanced. The walking tasks included 30 trials each with the following within-subjects variables: visibility (3 levels: 1 step ahead, 2 steps ahead, 3 steps ahead) and foot (2 levels: dominant, non-dominant). We recorded foot placement error on each stepping target. In the stepping task, there were 20 trials with 2 within-subjects variables: foot (2 levels: dominant, non-dominant) and vision (2 levels: available, occluded). For both the walking and stepping tasks, we randomised the visual conditions and the foot used across trials.

3.5.3 Analysis

We used mixed model ANOVAs to analyse our data. For the walking task: visibility (1, 2, 3 steps ahead) x foot (dominant, non-dominant) x threat (high, low) x age (adult, child). For the stepping task: foot (dominant, non-dominant) x vision (available, occluded) x threat (high, low) x age (adult, child). Significant interactions were further analysed using Bonferroni-corrected post-hoc tests. We applied a Greenhouse Geisser correction where the sphericity assumption was not met. Error values are given in centimetres. Time values are given in seconds. We used an ANCOVA analysis to look for effects of balance on foot placement error as an additional exploratory analysis.

3.6 Results – Study 2.2.

3.6.1 H1 (Walking) - In the flat condition, error will be higher when vision is restricted to just 1 step ahead. In the raised condition, error will be lower when vision is restricted to just 1 step ahead.

H1 was not supported. There was no significant interaction between threat and visibility for absolute error (p=.538) or variable error (p=.175).

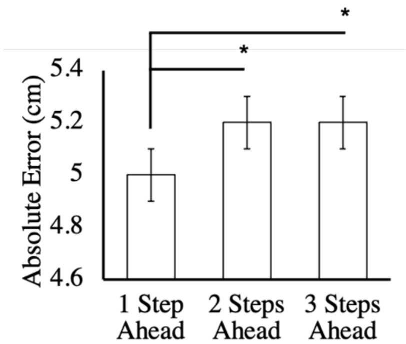

Figure 3. 9. Study 2.2 mean foot placement absolute error (cm) in each of the visibility conditions of the walking task. Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant differences between visibility conditions are indicated by asterisks.

However, there was a main effect of visibility on absolute error (irrespective of postural threat), $F(2, 88)=9.785$, $p<.001$, $\eta p^2=0.182$ (Figure 3. 9). Absolute error was significantly lower in the 1 step ahead condition (M=5.0cm, SE=0.1cm) compared to the 2 steps ahead condition (M=5.2cm, SE=0.1cm) $p<.001$, or the 3 steps ahead condition (M=5.2cm, SE=0.1cm) p=.006. There was no significant difference in absolute error between the 2 steps ahead and 3 steps ahead conditions p=1.00.

3.6.2 *H2 (Walking) – Time to complete each trial will be lower given 2 or 3 visible upcoming targets.*

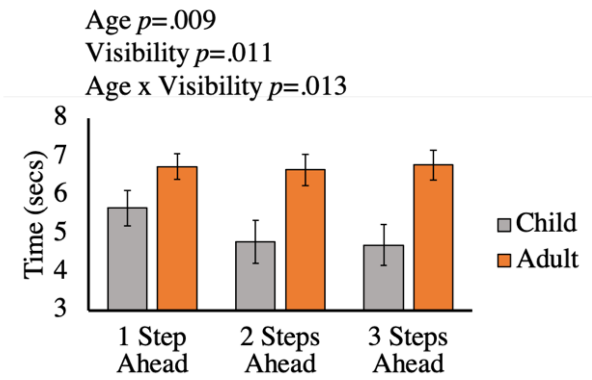

Figure 3. 10. Study 2.2 mean time taken to complete each trial (secs) for children and adults, given for each of the visibility conditions of the walking task. Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant main effects and interactions (with *p* values) are listed at the top of the figure.

As predicted (H2), there was a significant effect of visibility on time $F(2, 88)=5.263$, $p=.011$, $\eta p^2=0.107$ (Figure 3.10). Participants took significantly longer to complete each trial in the 1 step ahead condition (M=6.2secs, SE=0.3 secs) compared to the 2 steps ahead condition (M=5.7 secs, SE=0.4 secs) $p=.002$, or the 3 steps ahead condition (M=5.7secs, SE=0.3 secs) $p=.02$. There was no significant difference in time between the 2 steps ahead and 3 steps ahead conditions $p=1.00$.

However, further analysis reveals an interaction between visibility and age on time, $F(2, 88)=5.067$, $p=.013$, $\eta p^2=0.103$ (Figure 3.10). For adults, there was no significant effect of visibility on time $p=.846$. For children, there was a significant effect of visibility on time, $F(2, 15)=27.250$, $p<.001$, $\eta p^2=0.645$. Children took longer to complete each trial in the 1 step ahead condition (M=5.7secs, SE=0.3 secs) than the 2 steps ahead condition (M=4.8secs, SE=0.3 secs) $p<.001$, or the 3 steps ahead condition (M=4.7 secs, SE=0.2 secs) $p<.001$. There was no significant difference in children's time to complete each trial in the 2 step ahead condition compared to the 3 steps ahead condition $p=1.00$. Overall, children took significantly less time (M=5.1secs, SE=0.5secs) to complete each trial than adults (M=6.7, SE=0.4secs), $F(1, 44)=7.48$, $p=.009$, $\eta p^2=0.145$ (Figure 3.10).

3.6.3 H3 (Walking) - Children's error will be higher than adults'.

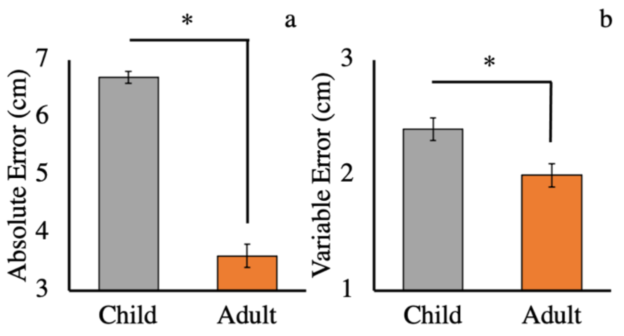

Figure 3. 11. Study 2.2 mean foot placement error (cm) for children and adults on the walking task – absolute error (a), variable error (b). Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant differences between children and adults are indicated by asterisks.

H3 was supported. Children's absolute error (*M*=6.7cm, *SE*=0.2cm, $F(1, 44)=156.296$, $p<.001$, $\eta p^2=0.78$; Figure 3. 11a) and variable error (*M*=2.4cm, *SE*=0.1cm, $F(1, 44)=12.445$, $p=.001$, $\eta p^2=0.22$; Figure 3. 11b) were significantly higher than adults' (absolute - *M*=3.6cm, *SE*=0.1cm; variable – *M*=2.0cm, *SE*=0.1cm).

3.6.4 H4 (Walking) – For adults only, error will be lower in the raised condition

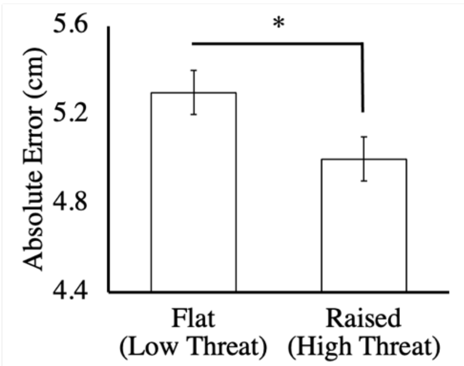

Figure 3. 12. Study 2.2 mean foot placement absolute error (cm) in the flat and raised conditions of the walking task. Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant difference between flat and raised condition is indicated by an asterisk.

H4 was not supported. There was no interaction between age and threat for absolute error ($p=.45$) or variable error ($p=.063$). In contrast, absolute error was significantly higher in the flat condition (*M*=5.3cm, *SE*=0.1cm) than the raised condition (*M*=5.0cm, *SE*=0.1cm) for both adults and children, *F*(1, 44)=10.411, *p*=.002, ηp^2=0.191 (Figure 3. 12).

3.6.5 *H5a (Stepping) – Error will be higher for children than adults*

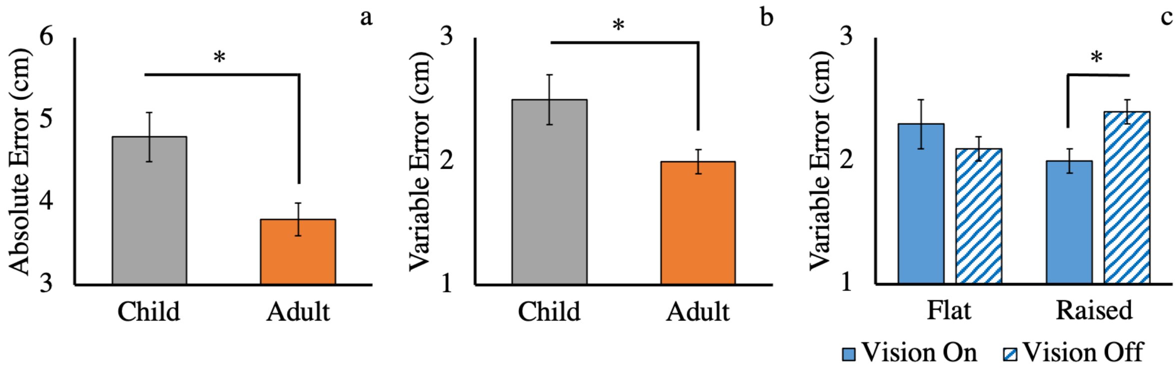

Figure 3. 13. Study 2.2 mean foot placement error (cm) on the stepping task – absolute error for children and adults (a), variable error for children and adults (b), variable error in the flat and raised conditions, for both visual conditions (c). Error bars represent standard errors. Note: to show significant differences more clearly, the y axis does not start at zero. Significant differences between children and adults, or between vision conditions are indicated by asterisks.

As predicted (H5a), children showed significantly higher absolute error (*M*=4.8cm, *SE*= 0.2cm) than adults (*M*=3.8cm, *SE*= 0.3cm), *F*(1, 44)=10.008, *p*=.003, ηp^2=0.185 (Figure 3. 13a). Children's variable error (*M*=2.5cm, *SE*=0.2cm) was also significantly higher than adults' (*M*=2.0cm, *SE*= 0.1cm), *F*(1, 44)=5.675, *p*=.022, ηp^2=0.114 (Figure 3. 13b).

3.6.6 *H5b (Stepping) - Error will be higher in the flat condition than the raised condition*

Contrary to H5b, there was no significant effect of threat on absolute or variable error (*p*'s > .7). However, there was a significant interaction between threat and vision on variable error, *F*(1, 44)=4.268, *p*=.045, ηp^2=0.088 (Figure 3. 13c). In the flat condition, there was no significant effect of vision (*p*=.37). However, in the raised condition, variable error was significantly higher with vision occluded (*M*=2.4cm, *SE*=0.1cm) than with vision available (*M*=2.0cm, *SE*=0.2cm), *p*=.049.

3.6.7 *Additional Findings – Study 2.2.*

Children had significantly poorer static balance (*M*=6.9 secs, *SE*=1.3 secs) than adults (*M*=37.7 secs, *SE*=3.0 secs) *t*(44)=7.244, *p*<.001. Children also had significantly poorer dynamic balance (*M*=11.7 steps, *SE*=1.1 steps) than adults (*M*=19.9 steps, *SE*=0.1 steps), *t*(44)=10.155, *p*<.001. To establish whether balance had an impact on stepping error, we calculated partial correlations, controlling for age. There was only one significant correlation between the balance measures and absolute stepping error, namely, between static balance and absolute error for single steps with the non-dominant foot, in the flat condition when vision was occluded, r=.346, p=.02; all other correlations were not significant (p's>.1). For the walking task, we included both static and dynamic balance as covariates (ANCOVA) and found no significant effect of static or dynamic balance on absolute stepping error p's>.2.

Absolute error (walking task) was significantly higher for the non-dominant foot (M=5.3cm, SE=0.1cm) than the dominant foot (M=5.0cm, SE=0.1cm) $F(1, 44)=5.220$, p=.027, $\eta p^2=0.106$.

Finally, for the walking task we conducted Pearson's correlations to see if children's absolute error (averaged across both the dominant and dominant foot) correlated significantly with time to complete trial. We would expect this since children reduced speed and foot placement error when visual information was restricted to just 1 step ahead. However, there was no correlation between absolute error and time to complete the trial in any of the visibility conditions for either the flat condition (p's>.7) or the raised condition (p's>.1).

3.6.8 Results Summary and Discussion – Study 2.2.

For our first hypothesis (H1), we expected that in the flat condition, restricting vision to just 1 step ahead would increase error. In the raised condition, we expected restricting vision to just 1 step ahead would be associated with lower error (as per study 2.1). On the contrary, in both high and low threat conditions participants demonstrated caution by reducing foot placement error when they could not see at least 2 steps ahead. Children also took longer to complete each trial when they could not plan at least 2 steps ahead. This partially supports H2, although we had predicted that adults would also slow down when visual input was restricted. In support of H3, children placed their feet less accurately and more variably than adults during walking. Finally, we expected that error during walking would be lower in the raised condition for adults (H4). In fact, we found that both children and adults reduced their error when walking in the more threatening raised condition.

On the single step task, children showed higher absolute and variable error than adults for single steps (supporting H5a). However, contrary to H5b, there was no main effect of postural threat on single step error.

The results of study 2.2 align with those of study 2.1. Both children and adults behave more cautiously when they cannot plan ahead and under conditions of postural threat. Interestingly, children and adults show the same level of feedforward planning in both the low and high threat conditions.

3.7 Discussion

We investigated whether 8-year-old children use vision in a feedforward manner to plan ahead during walking like adults, or whether children control walking one step at a time. We also tested whether visually guided walking behaviour would be affected by postural threat. Both children and adults reduced foot placement error and walking speed when visual information about the upcoming terrain was restricted to just 1 step ahead. Children made these adaptive changes despite their foot placement being both less accurate and more variable than adults' overall. When walking under conditions of postural threat, both children and adults demonstrated caution by reducing foot placement error.

3.7.1 Children and Adults Use Vision in a Feedforward Manner to Control Walking

Children control walking in a feedforward manner like adults. In study 2.1, we found that both children and adults walked more slowly when they could not see more than 2 steps ahead. Adults also placed their feet more accurately and less variably when visual information was restricted. In study 2.2, we replicated this finding: both children and adults reduced foot placement error (absolute and variable) when vision of the upcoming terrain was restricted to just 1 step ahead. In study 2.2, children (but not adults) also slowed down when they could not plan ahead. In summary, both children and adults behave cautiously (placing feet more carefully and walking more slowly) when they are unable to plan at least 2 steps ahead. Note that we did not find significant correlations between foot placement accuracy and time to complete trials. Therefore, we do not claim that changes in walking speed were directly related to foot placement error. In other words, we do not claim a speed accuracy trade-off at the individual participant level.

Previous work has shown that 2 steps ahead is an important visual window for adaptive walking. According to the critical control phase hypothesis (Matthis et al., 2017), a walker needs visual input from the foothold N, during step N-2. Our results support the critical control phase hypothesis in that when participants could not see at least 2 steps ahead, they tended to walk more slowly. This indicates that, for both children and adults, the preferred mode of control is to visually sample from at least 2 steps ahead. According to Matthis et al (2017), this allows the walker to plant step N-2 in such a way that the walker can reach step N by relying predominantly on passive forces and momentum.

Matthis and colleagues have also consistently shown that when visual information is restricted to less than 2 steps ahead, adults show increased foot placement error (Matthis et al., 2015, 2017) and increased obstacle collisions (Matthis & Fajen, 2014; Matthis & Fajen, 2013). In other words, when adults cannot plan at least 2 steps ahead, they struggle to walk adaptively. Our results tell a different story. When children and adults could not plan at least 2 steps ahead, they exercised caution, reducing both walking speed and foot placement error. Despite the contrasting patterns of results, the two sets of work agree that walking is controlled in a feedforward manner, with 2 steps ahead a particularly important visual window. Crucially, we demonstrate the importance of the 2 steps ahead visual window in children.

One reason for the contrast between our findings and those of Matthis and colleagues could be that in our VR task, participants did not have vision of their legs (only of their virtual feet). This lack of peripheral visual input from the lower body may explain why our participants behaved with such caution in both the 1 step ahead condition, and during high postural threat. Previous research suggests that peripheral input from the lower body plays a role during walking in complex terrain. Patla (1998) asked adults to walk toward and over an obstacle either with full vision or whilst wearing glasses which occluded the lower visual field. With the lower visual field occluded, participants placed their feet further away from the obstacle before crossing it and raised their toe higher (and more variably) over the obstacle. These behaviours are hallmarks of caution – leaving a larger margin of error around an obstacle. Crucially, other research shows that adults visually fixate obstacles in advance of crossing and not during crossing (Patla & Vickers, 1997). Therefore, the cautious behaviour observed by Patla (1998) can be specifically attributed to the loss of peripheral visual information about the legs (as opposed to the obstacle which could still be visually sampled in advance). Similar findings were obtained by Marigold and Patla (2008) – when adults walked over complex, multi-surface terrain wearing glasses occluding the lower visual field, walking was slower and steps were shorter. In the present study, the lack of peripheral visual input from the legs may explain the cautious behaviour shown by participants when they were unable to plan ahead at least 2 steps ahead, and when in conditions of postural threat. Nonetheless, we have shown that even under challenging VR conditions (without the usual peripheral visual input from the lower body) the 2 steps ahead feedforward sampling strategy is robust.

The feedforward strategy is robust across tasks in both adults and children. Previous work showed that children visually fixate obstacles a few steps ahead of obstacle encounters (Franchak & Adolph, 2010), reduce walking speed in preparation for obstacle crossing (Berard & Vallis, 2006) and place their feet differently before an obstacle depending on the upcoming obstacle sequence (Mowbray & Cowie, 2020). In obstacle-based tasks, children use vision in a feedforward manner, making anticipatory adjustments in response to the upcoming terrain. The present study adds that children also use vision in a feedforward manner to control walking when the feet must be placed into specific, tightly constrained positions. Children make adaptive changes to foot placement and walking speed when they are unable to plan at least 2 steps ahead. Like adults, children behave cautiously when feedforward visual sampling is not possible.

However, when visual information was available from 2 or 3 steps ahead, both adults and children showed higher foot placement error. Our participants' behaviour was similar to that observed in older adults at high risk of falling. High fall risk older adults prioritise visual planning for upcoming steps over accurate placement of the current step (Chapman & Hollands, 2007). They look away from the current stepping target prematurely, which is associated with higher foot placement error (Chapman & Hollands, 2007). The participants in the present study also seemed to have been using distal visual cues to increase walking speed, but at the expense of accurate foot placement. When participants had visual information from at least 2 steps ahead, foot placement error increased. We reiterate that this demonstrates both children's and adults' walking behaviour is influenced by distal visual cues.

Even in our simple, single step task we found evidence that adults and children use vision in a feedforward manner. Occluding the target at step onset had no effect on adults' or children's step accuracy and no effect on step variability (except in the raised condition of study 2.2). This suggests that children and adults were not habitually reliant on continuous, online visual feedback to control single stepping movements. They could step just as accurately whether the target was visible throughout the movement or not. This indicates that participants were using vision in a feedforward manner – visually sampling the target before step initiation. This contrasts with previous work which has found both adults and children use online visual feedback to fine-tine target-directed stepping movements (Mowbray et al., 2019; Reynolds & Day, 2005a; Study 1). Our finding was unexpected but could be explained by the VR paradigm. Previous work occluded vision completely during the step: participants had no visual information at all after foot-off (Mowbray et al., 2019; Reynolds & Day, 2005a; Study 1). In the present study, we occluded only visual information of the foot and target. Participants maintained visual information about the environment throughout the stepping movement. This additional, constant visual information could have helped participants to maintain balance and to remember the location of the target, even once the target was rendered invisible.

3.7.2 Foot Placement Error During Walking is Not Adultlike at Eight Years

Previous work showed that 8-year-olds' foot placement error was not significantly different from adults' for single steps to a target (Mowbray et al., 2019; Study 1). Therefore, we expected that 8-year-olds might also show similar foot placement error to adults during walking. However, in study 2.1 children's foot placement during walking was significantly less accurate than adults'. In study 2.2 children's foot placement during walking was both more variable and less accurate than adults'. This suggests that walking in a complex environment is challenging for children, even at 8 years. This compliments work by Corporaal et al (2018) who found that variability of foot placement onto targets during treadmill walking continues reducing even into adolescence. However, we acknowledge that in our VR paradigm, children's error was significantly higher than adults' even on a simple, single step task. It is possible that the VR environment was particularly challenging for children.

There are a number of differences between VR and real-world based tasks. Firstly, VR requires children to learn a new visuomotor mapping between their own motor commands and proprioception, and the new visual image of the virtual foot. We know from visuomotor adaptation paradigms that this type of remapping is a relatively new achievement at 8 years (Contreras-Vidal et al., 2005). We also know that the size of our own body parts are an important cue for understanding the spatial layout of the environment (Linkenauger et al, 2013). Children may have found it more challenging than adults to learn new relationships between the novel virtual foot and the virtual world in the absence of other body cues (such as the legs which were not visible in VR). Secondly, VR may be particularly exciting for children. If children are in a state of greater excitement than adults, this could lead to differences in behaviour. Finally, wearing a headset could affect children differently to adults in terms of balance, especially if the headset is proportionately heavier for children. We know that children's balance was poorer than adults' even before wearing the headset (see additional findings of study 2.1 and study 2.2) and previous work has shown that even among adults, being in an immersive virtual scene can increase postural sway to a similar extent as standing with eyes closed (Horlings et al., 2009). However, our analyses showed that there was no significant relationship between balance and foot placement error for walking or single steps. Despite all of these issues, children did demonstrate sophisticated visually guided planning. Even in a novel VR environment, children can use distal visual cues to adjust their walking behaviour like adults.

3.7.3 Children and Adults Respond to Postural Threat with Caution but Continue to Plan Ahead

Changing the level of postural threat had a significant impact on both children's and adults' behaviour. In study 2.2, both children and adults showed lower foot placement error in the raised (high threat) condition compared to the flat (low threat) condition. In other words, when walking in conditions of postural threat, participants demonstrated caution by stepping more carefully. How might participants have achieved this without also reducing walking speed in high postural threat environments? It is likely that participants lowered foot placement error by upregulating proprioception. Previous work has shown that muscle spindle sensitivity increases under conditions of threat, such as standing at the edge of an elevated platform (Davis et al., 2011). Further, participants report similar postural sway amplitude when standing at height (high threat), even though this high threat condition is associated with objectively lower sway amplitudes than low threat conditions (Cleworth & Carpenter, 2016). The authors argued that this could be because in conditions of postural threat, proprioceptive sensory gain is increased (Cleworth & Carpenter, 2016). In other words, participants are able to access greater or more detailed proprioceptive information. Similar mechanisms could explain how participants in the present study lowered their foot placement error during the high threat condition.

Another possibility is that, under conditions of postural threat, participants adopted a more careful, toe-first foot placement style. This would contrast with the heel-first approach of normal walking. Kluft et al (2020) found that older adults were more likely to adopt a more energetically demanding (but safer) toe-first approach when descending a step on a raised platform (0.78m, high postural threat). In contrast, when descending a step at ground level (low postural threat), they adopted a more energy efficient heel-first strategy. However, step descent is a very different task than walking over targets. Future work should directly measure the way in which participants place their feet (heel-first or toe-first) to establish whether the effects of postural threat observed by Kluft et al (2020) can also be observed during walking over targets and among children and young adults.

Our results around postural threat contrast with those of Ellmers and Young (2019) who found that young adults' foot placement error was not affected by postural threat (raised walkway 1.1m above ground vs flat ground). Further, they found that during conditions of threat, participants tended to use an online mode of control; looking at the immediate walkway in front of them (Ellmers & Young, 2019). In contrast, we found that both children and adults engaged in feedforward visual control, even in high threat conditions. This difference in findings might be explained by methodological differences. For example, Ellmers and Young (2019) used stepping targets with raised edges (a small box around the target which participants had to step inside of). They took this approach to encourage accurate stepping. However, this design also imposes a degree of postural threat even in the baseline (low threat) condition. In our study 2.2, the flat (low threat) condition did not include any raised elements. Therefore the flat (low threat) condition in the present study may have been even lower in postural threat than the low threat condition used by Ellmers and Young (2019). This could explain why we found a significant difference in foot placement error between high and low threat conditions, whilst Ellmers and Young (2019) did not.

3.8 Conclusions

When walking in a complex environment, 8-year-olds use vision in a feedforward manner to plan ahead like adults. When visual information about the upcoming terrain is restricted to just 1 step ahead, both adults and children behave cautiously: they slow down and place their feet more accurately. Building on the work of Matthis and colleagues, we show that 2 steps ahead is an important visual window for both children and adults during walking. This is true for both high and low postural threat environments. When postural threat is high, both children and adults respond with caution, reducing foot placement error. Despite their sophisticated adjustments to walking, 8-year-old children's foot placement error remains higher than adults', both during walking and for simple, single steps.

3.9 Moving from Vision to Proprioception

In part 1 of this thesis, we focused on visual control of stepping and walking. Nonetheless, proprioception plays a key role in these behaviours and is important in our interpretation of the findings of both studies 1 and 2. In study 1, we argued that improvements in proprioceptive control may contribute to the development of precision stepping performance. We found equal visual reliance for stepping at 6, 7, and 8 years. We also saw improvements with age in both visually guided and non-visually guided stepping. Therefore, developmental improvement in step accuracy could not be explained by improving use of visual feedback. Other factors, including proprioception, must be at play. In study 2, we argued that the upregulation of proprioceptive inputs might explain how participants were able to reduce foot placement error when walking in conditions of postural threat (Cleworth & Carpenter, 2016; Davis et al, 2011). Further, because the legs were not visible in our VR paradigm, participants faced additional proprioceptive challenges: to control the legs without visual feedback and to learn a new sensory mapping between motor commands and proprioceptive feedback, and the new visual representation of the virtual foot. By successfully walking over complex terrain in this VR set-up, both adults and children demonstrated a high level of proprioceptive ability. Even in more natural scenarios, the preferred visual strategy of adults is to plan ahead – not to visually monitor and control each individual step 'online' (Matthis et al, 2018). Therefore, leg movements must be guided (at least in part) proprioceptively. Indeed, individuals experiencing proprioceptive loss have significant difficulty with balance and walking (Sainburg et al, 1993). Given the many ways in which proprioception is crucial for movement, we focus on proprioceptive control in part 2 of this thesis.

Before moving on to part 2 of this thesis (proprioception) we will summarise the findings of part 1 (visual control).

3.9.1 Summary of Part 1 – Visual Control

In part 1, we focused on visually guided action. In study 1, we found that the reaching and stepping movements of children aged 6, 7, and 8 years were visually guided to the same extent as adults'. Whilst both being visually guided, stepping and reaching had different developmental profiles. Further, we found that by 8 years children's stepping movements were as accurate and precise as adults'. In study 2, we wanted to find out whether 8-year-olds would also show adultlike visually guided walking (a more complex, whole-body task). We found that both children and adults behave cautiously when they cannot use vision to plan ahead, by reducing walking speed and foot placement error. They achieve this in both high and low postural threat environments. We draw the following conclusions from studies 1 and 2.

Visually guided action develops in a limb specific manner. Whilst both stepping and reaching are visually guided in childhood, their developmental profiles are different. Stepping error reduced between 6 and 8 years, whilst reaching error was lower and stable between 6 and 8 years. This emphasises the need for a whole-body approach in developmental research – control of the arms and legs does not develop synchronously.

Children use online visual feedback and use vision in a feedforward manner depending on the task. Children demonstrate sophisticated visual control strategies, even before they have adultlike movement accuracy and precision. Children tailor their visual strategy depending on the demands of the task and the environment. When a task demands very precise, single stepping movements, children use continuous online visual feedback to fine-tune the step trajectory. When the task demands walking in a complex environment, children use distal visual cues to plan ahead. When vision is restricted such that planning ahead is not possible, children exercise caution by slowing walking speed and reducing foot placement error. In summary, children demonstrate flexible, adaptive behaviour in the face of changing task and environmental conditions, facilitated by visual sampling.

Adultlike performance on a simple, single limb task does not necessitate adultlike performance on a related complex, whole-body task. Children's foot placement error for simple, single stepping movements was not significantly different to adults' . However, during walking their foot placement error was significantly higher than adults. Therefore, we emphasise the importance of using complex, whole-body tasks to understand sensorimotor development. On one hand, more complex tasks highlight that children's sensorimotor control may still be immature. On the other hand, more complex tasks highlight children's sophisticated abilities that would otherwise not be observed.

3.9.2 Introducing Part 2 – Proprioceptive Control

Vision is clearly crucial for adaptive movement control. However, it is not the only sensory input that we use to control movement. In study 1, we argued that immature proprioception might be one of many factors that explains why step accuracy and precision take a long time to mature. In study 2, we speculated that the up-regulation of proprioception might explain how participants reduced foot placement error under conditions of postural threat. In part 2 of this thesis, we further explore the development of proprioception.

In study 3, we investigate the specific cues that children use to make memory-based proprioceptive judgements for both the arms and the legs. Specifically, we ask whether children do or do not use feedforward predictions when making single limb proprioceptive judgements. In study 4, we conducted a non-randomised control study to explore whether creative dance sessions could improve children's whole-body proprioception.

Part 2 – Proprioceptive Control

Chapter 4

Study 3 - The Development of Forward Models for Proprioceptive Memory

4.1 Introduction

4.1.1 Forward Models for Proprioception in Adults

Proprioception (the sense of body position) arises both from feedback mechanisms providing sensory information from the muscles, skin and joints, and from feedforward mechanisms which use 'forward models'. A forward model is a prediction of the body's future state, based on knowledge of the body's current state and knowledge of live motor commands to the body (Miall & Wolpert, 1996). In adults, differences between this predicted state and the actual state can be fed back into the model, to improve motor accuracy and inform rapid movement adjustments (Miall & Wolpert, 1996). Forward models are generated for active (self-generated) movement. Active movement activates a large set of neural areas including: M1 and S1, sensorimotor and premotor cortex, supplementary motor area, secondary somatosensory areas, basal ganglia and the cerebellum (Jaeger et al., 2014; Kawato et al., 2003; Mima, Sadato, Yazawa, Hanakawa, & Fukuyama, 1999; Wolpert et al., 1998). In contrast, passive (externally-generated) movements are associated with lesser neural activation (Jaeger et al., 2014), may activate somatosensory areas only (Mima et al., 1999) and are not associated with forward model generation.

Numerous adult studies use a 'target and report' proprioceptive memory paradigm to study forward models. In the target phase, participants experience a target arm movement actively (both sensory feedback and a forward model generated) or passively (sensory feedback only). In the report phase, participants attempt to actively reproduce the target movement from memory. Vision of the arm is occluded throughout. Adults report with lower error following active target movement (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). Training of the forward model during an active target movement improves movement accuracy in the report phase.

Before moving onto the developmental literature, we must highlight some nuances. Firstly, not all proprioceptive tasks show clear benefits of forward models in adults. For example, both Capaday, Darling, Stanek and Van Vreeswijk (2013) and Darling, Wall, Coffman and Capaday (2018) found that blindfolded adults could point to their own finger with the contralateral finger equally well whether the target finger was positioned actively (self-movement) or passively (arm moved by experimenter). This task does not rely on memory like the above-mentioned 'target and report' style tasks. Capaday et al and Darling et al argue that their natural, unconstrained task does not require forward models. They go even further in stating that the hypothetical construct of forward models may be unnecessary (Capaday et al., 2013) and that forward models may not even exist (Darling et al., 2018). In contrast, tasks with more complex memory demands benefit from forward models generated during active movement. Secondly, it would be an oversimplification to say that passive movements are not in any way associated with error detection and correction (processes attributed to forward model mechanisms). Passive movement can be important for establishing a reference of correctness – an example of the 'perfect' movement against which active movement can be compared, facilitating error detection (Bested, de Grosbois, Crainic, & Tremblay, 2019). However, in a constrained target and report paradigm (as per the present study) active and passive target movements are matched in terms of direction and amplitude. Therefore, both the active and passive target movement provide an equally 'correct' demonstration of the target movement. The only difference is that the active movement generates a forward model, whilst passive movement does not.

4.1.2 Forward Models for Proprioception in Children

Whilst it is widely accepted that adult movement and memory-based proprioceptive judgements benefit from forward models, we do not know whether the same is true for children. Forward models originate in the cerebellum (Wolpert et al., 1998). During active movement, forward models benefit the proprioceptive performance of healthy adults, but not those with cerebellar damage (Bhanpuri et al., 2013). Prenatally, the cerebellum develops very rapidly (Volpé, 2009). Therefore, infants may possess the basic neural architecture necessary for forward model generation. However, the most useful question is not whether children have the basic capacity to generate forward modes at all, but whether children's task performance *benefit*s from forward models. Significant benefit from effective forward models might plausibly come later, especially since the cerebellum continues developing throughout childhood, only reaching peak volume after 11 years (Tiemeier et al., 2010). Thus, we have two competing hypotheses: i) that children do benefit from forward models, ii) that children do not benefit from forward models.

We argue that there is a gap in the developmental literature on proprioception: a need for a simple, but direct manipulation of forward model availability using active and passive movement. In the present study, we use exactly this approach to explore whether children benefit from forward models for memory-based proprioceptive judgements. We will now discuss developmental studies that have made suggestions about childhood forward models in the context of proprioception via three paradigms:

sensorimotor adaptation, tendon vibration, and speed-based tasks. These approaches are not necessarily memory-based, but nonetheless provide useful insight into the development of proprioception and forward models.

4.1.3 Sensorimotor Adaptation

In sensorimotor adaptation tasks children draw to targets without *direct* visual feedback of the drawing hand, relying on proprioceptive cues only. Digitised visual feedback of the drawing hand is rotated. When visual feedback is subsequently restored to normal, participants may show after-effects. These after-effects manifest as biases in drawing angle (initial direction error; IDE) caused by a new visuo-proprioceptive mapping, formed by updating forward models to accommodate the rotation. Such after-effects have been found at 5- to 12-years, suggesting that children do update forward models to accommodate rotated sensory feedback (Deng, Chan, & Yan, 2019; Kagerer & Clark, 2014). Another study by Musselman, Roemmich, Garrett and Bastian (2016) found after-effects in children's step synchrony after walking on a split-belt treadmill and then returning to a synchronous treadmill belt. This indicates that children can also adapt an internal model for leg movements. However, the extent of the positive benefit is questionable. Children are slower than adults to re-adapt once the feedback rotation is removed (Deng et al., 2019; Kagerer & Clark, 2014). Further, it is possible that children solve adaptation tasks (e.g. Deng et al., 2019; Kagerer & Clark, 2014; Musselman et al., 2016) using explicit, cognitive strategies without necessarily updating forward models (Deng et al., 2019; McDougle, Ivry, & Taylor, 2016).

Other work found no IDE after-effects until 8 years, suggesting younger children do not benefit from forward models (Contreras-Vidal et al., 2005). However, younger children may not show after effects because they view their directional errors as normal, i.e. within the realms of their usual highly variable movement (Contreras-Vidal et al., 2005). Indeed, younger children's performance is highly variable on aiming tasks, even without rotation (Contreras-Vidal, 2006). Consequently, young children may not demonstrate forward model use simply because they do not seek to correct their errors (Contreras-Vidal et al., 2005). Accordingly, a simpler task with fewer degrees of freedom may attenuate this confound by reducing movement variability and provide a more robust test of whether young children do or do not benefit from forward models. We adopted this approach in the present study.

4.1.4 Tendon Vibration

Other studies have used tendon vibration to directly disrupt proprioceptive feedback, leaving forward models as a remaining cue to limb position. Tendon vibration applied either during or before target-directed movements (without vision of the hand) induced error at all ages (5, 7, 9, 11 years), but to a greater extent among 5-year-olds (Hay & Redon, 1997; Hay, Bard, Ferrel, Olivier, & Fleury, 2005).

The authors argue that, with age, children become better able to combine and alternate between feedback and feedforward strategies (Hay & Redon, 1997; Hay et al., 2005).

However, there are multiple interpretations of younger children's poor performance. A child may perform poorly because they do not generate a forward model and attempt the task with only unreliable sensory feedback. Alternatively, a child may use a forward model, but still perform poorly because a good forward model needs accurate sensory feedback to compute the body's current state and to compare against predicted feedback to generate error signals (Miall & Wolpert, 1996). Older children may overcome these challenges with explicit strategies (Deng et al., 2019; McDougle et al., 2016). But where performance is poor, we cannot be sure whether or not forward models are involved. In short, disrupting sensory feedback may also disrupt forward models. We could overcome this limitation by directly manipulating the availability of a forward model, whilst keeping sensory feedback constant. This was the approach taken in the present study.

4.1.5 Speed-based Tasks

Very rapid movements can only be controlled effectively if a forward model is employed, since sensory feedback loops alone are too slow to allow fast enough movement updating (Miall & Wolpert, 1996). When reaching without vision of the hand, 8 year olds rapidly update movements in response to sudden shifts in target location much more effectively than younger children (Wilson & Hyde, 2013). Between 6 and 11 years, children show increased speed and smoothness when manually tracking a fast moving dot, although 6- to 9-year-olds struggle at high velocities (Van Roon, Caeyenberghs, Swinnen, & Smits-Engelsman, 2008). The authors argue that, with age, children replace a slow feedback-based strategy with a faster, smoother feedforward approach (Van Roon et al., 2008; Wilson & Hyde, 2013).

However, there are numerous alternative explanations for these findings. Firstly, development may be driven by improving domain-general information processing speed (Hale, 1990; Van Roon et al., 2008). Secondly, sensory feedback must be compared with predictions to build an accurate, useful forward model (Wolpert & Flanagan, 2001). Therefore, poor performance could be explained by poor sensory feedback processing, preventing younger children from building and calibrating useful forward models (Smits-Engelsman, Wilson, Westenberg, & Duysens, 2003). Thirdly, improvements in the variability of motor output could explain developmental improvements on speed tasks (Contreras-Vidal, 2006; Van Roon et al., 2008). Without directly manipulating the availability of forward models, we cannot clearly understand whether forward models do or do not benefit children's performance.

4.1.6 The Gaps in the Developmental Literature

Using sensorimotor adaptation (Deng et al., 2019; Kagerer & Clark, 2014; Musselman et al., 2016), tendon vibration (Hay & Redon, 1997; Hay et al., 2005), and speed-based paradigms (Van Roon et al., 2008; Wilson & Hyde, 2013) researchers have suggested that children may be benefitting from forward models for proprioception and that forward model use improves through childhood. However, development in movement variability, sensory and information processing, and explicit cognitive strategies represent potential alternative explanations for previous findings.

An important contribution to the developmental literature will be a direct manipulation of forward model availability during a target and report memory-based proprioceptive task, using an active/passive movement comparison akin to that used in the adult literature (Adamovich., et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). This will indicate clearly whether removing the opportunity for forward model generation impacts on children's proprioception or not (at least in a memory-based proprioceptive task). Importantly, this approach allows sensory feedback to remain constant both with and without a forward model present.

Further, the current proprioception literature (both adult and developmental) focuses largely on the arms - with few exceptions, e.g. Musselman et al (2016). Natural movement is a whole-body phenomenon and we cannot assume that proprioceptive control of the upper and lower limbs would have the same developmental profile. Indeed, the developmental profiles of precise stepping and reaching movements are different (Mowbray et al., 2019; Study 1) and adults show more accurate proprioception with the arms than with the legs (Paschalis, Nikolaidis, Giakas, Jamurtas, & Koutedakis, 2009). We need to assess children's forward model use, and proprioception more broadly, for both the arms and legs. Previous developmental proprioceptive studies have measured children's ability to match target elbow angles (Goble et al., 2005; Holst-Wolf et al., 2016) or point to their own unseen body parts (Sigmundsson, Whiting, & Loftesnes, 2000; von Hoftsen & Rösblad, 1988). These studies show significant improvement in early childhood (before 8 years), with continued refinement into adolescence. However, none of these studies included the legs as the responding limb.

4.1.7 The Present Study

The primary aim of this study was to evaluate two opposing hypotheses: that children do benefit from forward models for memory-based proprioceptive judgements, or that they do not. As secondary aims, we explored the developmental profile of proprioception (4- to 14-years) and compared proprioception for the dominant vs. non-dominant limbs. We used a task in which participants tried to remember and reproduce target arm and leg positions. We measured absolute and variable error to gauge the accuracy and consistency of children's awareness of limb position in different conditions. Despite our critique of the existing developmental literature, there is a common suggestion that children do benefit from forward models on a variety of tasks. Therefore, our first hypothesis was that all participants would benefit from forward models (H1), with higher absolute and variable error in the passive condition (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). Both cerebellar development (Tiemeier et al., 2010) and proprioception (Holst-Wolf et al., 2016) have previously been shown to continue maturing into adolescence. Therefore, our second hypothesis was that there would be higher absolute and variable error among children than adults (H2a), and reducing absolute and variable error with age in childhood (H2b; Contreras-Vidal, 2006; Sigmundsson et al., 2000; von Hoftsen & Rösblad, 1988; Wilson & Hyde, 2013). Finally, research has consistently demonstrated that the dominant arm performs more poorly on proprioceptive tasks following passive movement, in both left and right handed adults (Goble et al., 2006, 2009; Schmidt, Depper, & Kerkhoff, 2013) and children (Goble et al., 2005). Therefore, our final hypothesis (H3) was that there would be greater absolute error for the dominant limb, for the largest movements (Goble et al., 2009), in the passive condition (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001).

4.2 Methods

4.2.1 Participants

Participants were 64 typically developing children (30 female) with mean age 8.6 years (range 4.4-14.5 years, *SD*= 2.1 years). Thirty-one children completed the task with their legs and had a mean leg length of 69.4cm (*SD*=8.9cm). Thirty-three children completed the task with their arms and had a mean arm length of 58.8cm (*SD*=6.3cm). Children were recruited via opportunity sampling and tested at a UK science museum. Forty-eight children were included in our final analyses (aged 4- to 13-years): more detail on the reasons for exclusion are given in the analysis section. Twenty adults (17 female) with a mean age of 23.8 years (range 19.4-31.2 years, *SD*=3.3 years), mean arm length of 72.7cm (*SD*=5.3cm), and mean leg length of 89.7cm (*SD*=5.4cm) were recruited via opportunity sampling and tested in the lab. Participants had no reported neurological or muscular deficits, developmental or coordination disorders, physical disabilities or significant visual impairments. We established hand and foot dominance by asking participants/parents which hand they/their child write(s) with and which foot they/their child would prefer to kick a ball with. The study was approved by the Durham University Psychology Department Ethics Committee and carried out according to the principles laid down in the 1964 Declaration of Helsinki

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4.2.2 Design

For adults, we used a within-subjects design with four within-subjects variables: limb type (arm or leg) and limb dominance (dominant or non-dominant), movement type (active or passive) and movement distance (large or small). Adults completed 4 blocks per limb, with 12 trials per block (48 trials in total). The order in which adults used their 4 limbs was randomised. Within each limb block, movement type and distance were randomised, with 3 trials for each of the 4 combinations. With children in contrast, we opted for a mixed design to reduce the required number of trials per participant – this was most practical given the science museum setting for the data collection. The two between-subjects variables were limb type and limb dominance. The two within-subjects variables were movement type and movement distance. Each child completed 12 trials in total with just one of their limbs. Movement type and distance were randomised across trials. Age in years was recorded as a continuous variable.

Movement distance was scaled to participant arm and leg length by sorting participants into bands according to limb length and scaling using the average value of the band (Table 4. 1). For the arms, small movement distance was 20% arm length and large movement distance was 35% arm length. For the legs, these values were 10% leg length and 17% leg length respectively. These distances could be comfortably achieved by all participants, without requiring maximum limb extension whilst also maximising the difference between the small and large distance conditions.

Table 4. 1.

Arm and leg length scaling.

Arms					
Band	Min limb length (cm)	Max limb length (cm)	Average limb length for band (cm)	Small distance 20% arm length (cm)	Large distance 35% arm length (cm)
1	40	51	45	09.00	15.75
2	52	62	57	11.40	19.95
3	63	73	68	13.60	23.80
4	74	84	79	15.80	27.65
Legs				Small distance 10% leg length (cm)	Large distance 17% leg length (cm)
1	40	58	49	04.90	08.33
2	59	77	68	06.80	11.56
3	78	96	87	08.70	14.79
4	97	115	106	10.60	18.02

4.2.3 Apparatus

Figure 4. 1. Apparatus. The arm or leg could be moved along a linear track passively or actively. A metal stopper could be placed at locations along the track. Digital display showed movement time and a ruler was used to measure distance moved.

A custom-built machine moved the limbs and measured responses (Figure 4.1). In the arm condition, the apparatus was placed on a table top. In the leg condition, the apparatus was placed on the floor. The apparatus consisted of a handle or foot rest (interchangeable) attached to a motorised track. In the passive movement condition, the apparatus moved the participant's limb along the track. Movement distance was selected using a digital display. In the active movement condition, the participant was able to push the apparatus along the track, with a physical stopper to signal the target position. The stopper could be placed at various points along the track. We used a built-in ruler for measuring the distance moved by the participant, and recorded and displayed movement time digitally.

4.2.4 Procedure

Participants were seated and blindfolded throughout. Participants using the arms sat close to a table such that their elbow was in a comfortable, bent position with the hand close to the side of the torso when the hand was in the start position, grasping the handle. Participants using the legs sat with one foot flat on the floor, the other on the apparatus foot rest, and their knee forming a 90 degree angle.

4.2.4.1 Target Phase. The limb was moved either passively or actively to a target position (defined by the physical stopper in the active condition) and back again. In the passive condition, we instructed the participant to relax their arm but to maintain grip of the handle. In the active condition, we instructed participants: "Slowly move your arm forwards until you feel it hit the stopper, then slowly move back to the start position". We encouraged participants to move at a similar speed as the apparatus in the passive condition. In both conditions, the apparatus recorded target phase movement time.

4.2.4.2 Report Phase. We removed the stopper (in the active condition). We instructed the participant as follows: Passive condition - "Now slowly move to where you think the robot stopped and stay there". Active condition - "Now slowly move to where you think the stop was and stay there". Participants did not receive performance feedback. The experimenter manually recorded the distance moved by the participant. We then instructed the participant to move slowly back to the start position.

4.2.5 Data Analysis

For each limb, participants should have each completed 3 trials per movement type/distance combination. Due to experimenter error in assigning conditions, not all children completed this. Since completing more trials might produce better performance due to learning, we analysed only the first 2 trials per condition for all participants (children and adults). Sixteen children had to be excluded, leaving a final sample of 48 children (25 female), with mean age 8.5 (4.4 - 13.7 years, *SD*=1.9 years). A full summary of participant characteristics is given in Table 4. 2.

Table 4. 2.

Participant characteristics.

Participants included in the analyses			N (number female)	Age (years) Mean(range)	SD	Arm length (cm) Mean(range)	SD	Leg length (cm) Mean(range)	SD
Children	Arms	Dominant	16 (8)	8.5 (5.6-10.5)	1.7	57.5 (48-68)	5.7	N/A	N/A
		Non-dominant	13 (8)	8.4 (6.7-10.2)	1.1	57.6 (52-69)	5.2	N/A	N/A
	Legs	Dominant	11 (7)	8.6 (4.4-13.7)	2.9	N/A	N/A	70.5 (53-93)	12.6
		Non-dominant	8 (2)	8.4 (6.4-11.8)	1.8	N/A	N/A	72.0 (64-82)	6.7
Adults			20 (17)	23.8 (19.4-31.2)	3.3	72.7 (66-86)	5.3	89.7 (84-101)	5.4

We calculated absolute error (mean unsigned distance between target and participant's movement end-point) and variable error (unsigned standard deviation of absolute error values). As a supplement, in Appendix 1 we also analyse constant error. For both adults and children, we analysed data from the arms and legs separately because the distances used for the arms and legs were not the same. Therefore, the tasks for the arms and legs were not directly comparable. Nevertheless, it is valuable to have data on both limbs to give a whole-body picture of motor control.

4.2.5.1 Statistical Analysis – Adults. We analysed the adult data for each error type separately (absolute and variable) using repeated measures ANOVA:

Movement Type (within) x Distance (within) x Dominance (within)

4.2.5.2 Statistical Analysis – Children. To reduce the risk of type 1 error in our mixed-ANCOVA design, we analysed the children's data using a hybrid ANCOVA-ANOVA method, recommended by Schneider, Avivi-Reich, & Mozuraitis (2015; Table 6, p. 11). For each error type separately (absolute and variable), we used the following procedures:

1) We centered the covariate (age) relative to mean age.

2) We ran an ANCOVA:

Movement Type (within) x Distance (within) x Dominance (between) x Age (covariate).

From this analysis, we extracted the relevant statistics for between-subjects effects, interactions of between-subjects and within-subjects effects, and interactions of the covariate and within-subjects effects.

3) We then ran a mixed-model ANOVA:

Movement Type (within) x Distance (within) x Dominance (between).

From this analysis, we extracted the relevant statistics for the remaining within-subjects effects. Within-subjects effects are independent of the covariate: for example, a child is the same age when they perform both the active condition and the passive condition (Annaz, Karmiloff-Smith, Johnson, & Thomas, 2009).

For all ANCOVA and ANOVA analyses, we followed-up significant interactions with Bonferroni-corrected post hoc tests. To compare adults' vs. children's error, we averaged across conditions and used a non-parametric Man Whitney *U* test since the sample size for adults and children were not balanced. We report 90% confidence intervals around effect size ηp^2 (Steiger, 2004), and 95% confidence intervals around effect size *r* (for Mann Whitney *U* tests).

4.2.6 Power Analysis

We conducted compromise power analyses using G*Power software version 3.1.9.2 (Faul et al., 2007) to establish the power of our sample sizes to detect medium sized effects (f=.03). We chose medium effect sizes (f=0.3; dz=0.5; d=0.5) for our power analysis based on previous literature. Many adult studies comparing active and passive movement conditions report large effect sizes. Erickson and Karduna (2012) report effects of 0.49 to 0.78. Adamovich, et al (1998) reported $F(2, 12)$=8.11: using resources from Lakens (2013) we calculated this to be a large effect size of ηp^2=0.57. Goble et al (2009) likewise reported a large effect size for significant interactions between arm dominance and movement amplitude (d=1.1). However, not all papers reported effect sizes or the statistics needed to calculate them. We cannot assume large effect sizes in studies which did not report them. Further, we were not aware of a comparable task in the developmental literature on which to base our effect sizes for children. Therefore, we used a conservative medium effect size in all of our power analyses for the child and adult data.

Since all of our variables had fewer than 3 levels, the sphericity assumption was not of concern. Therefore, we always used a non-sphericity correction of 1. Since we did not have previous data for this type of task with children or with adults using the legs, we used a conservative value of 0.1 for the correlation between repeated measures in our power analyses. Since the distances used for the arms and legs were not directly comparable, we calculated power for the arms (N=20 adults, N=29 children) and legs (N=20 adults, N=19 children) separately.

Our adult data was analysed using a 2 x 2 x 2 within-subjects ANOVA. We entered the following parameters: f=0.3, beta/alpha ratio=0.5, number of groups=1, number of measurements=8, correlation among repeated measures=0.1, non-sphericity correction=1. Our sample of 20 adults yields a power of 0.93 to detect a within-subjects effect of medium effect size.

Our children's data had a more complex mixed ANOVA - ANCOVA design. Therefore, it was necessary to conduct power analyses separately for each hypothesis.

H1 was a simple comparison of 2 within-subject conditions: main effect of movement type (active vs passive). Therefore, we examined power for a matched pairs repeated measures t-test (one tailed) using the following parameters: dz=0.5, and beta/alpha ratio of 0.5. For the arms, our sample of 29 yields a power of 0.94 to detect a medium within-subjects effect. For the legs, our sample of 19 yields a power of 0.90 to detect a medium within-subjects effect.

H2a was also a simple comparison of 2 groups (adults vs children) of unequal sample size. Given these unequal sample sizes, we examined power for a non-parametric Mann Whitney U test (one tailed). We entered the following parameters: normal parent distribution, d=0.5, beta/alpha ratio =0.5. For the arms, our sample of 20 adults and 29 children yields a power of 0.86 to detect a medium effect size. For the legs, our sample of 20 adults and 19 children yields a power of 0.85 to detect a medium effect size.

For H2b, we predicted that within children, age would correlate with error, producing a significant effect of age in an ANCOVA analysis. We conducted a power analysis for a correlation (bivariate normal model, one tailed) using beta/alpha ratio=0.5 and *p H0*=0. For the arms, our sample of 29 children yields a power of 0.86 to detect a medium correlation (*p H1*=0.3). For the legs, our sample of 19 children yields a power of 0.82 to detect a medium correlation (*p H1*=0.3).

H3 was a 3-way interaction: movement type (within-subjects) x distance (within-subjects) x dominance (between-subjects). For the power analysis, we broke the interaction down into the appropriate follow-up analyses. We split the data by distance (small/large). This renders two 2-way mixed ANOVAs (small distances: movement type x dominance, large distances: movement type x dominance). We entered the following parameters: *f*=0.3, beta/alpha ratio=0.5, number of groups=2, number of measurements=2, correlation among repeated measures=0.1, non-sphericity correction=1. For the arms, our sample of 29 children yields a power of 0.88 to detect a within-between interaction, 0.86 to detect a between factors effect, and 0.88 to detect within-subjects effects. For the legs, our sample of 19 children yields a power of 0.83 to detect a within-between interaction, 0.81 to detect a between subjects effect, and 0.83 to detect a within subjects effect.

4.3 Results

We present our results in relation to our hypotheses and predictions. We then present additional significant findings which were not predicted. A full summary of the means and standard errors is given in Tables 4.3 to 4.6.

Table 4. 3.

Absolute error for adults (means and standard errors in millimetres).

	Active							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	16.68	15.64	17.53	16.94	17.06	15.14	16.76	12.33
SE	2.04	2.38	2.99	2.18	1.80	2.30	2.13	1.34
	Passive							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	26.27	25.70	20.44	20.74	25.17	23.89	34.92	18.98
SE	3.38	3.57	3.03	3.40	2.67	3.32	5.93	2.14

Table 4. 4.

Variable error for adults (means and standard errors in millimetres).

	Active							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	13.26	11.11	12.44	15.51	14.65	9.70	15.88	10.80
SE	2.01	1.73	1.65	2.89	2.14	1.81	2.49	1.57
	Passive							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	16.71	15.76	20.20	13.68	18.76	15.35	26.68	12.51
SE	2.37	3.78	3.28	2.86	2.61	2.34	4.56	2.15

Table 4. 5.

Absolute error for children (means and standard errors in millimetres).

	Active							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	28.72	21.09	35.22	27.65	30.42	14.75	37.58	25.09
SE	4.09	4.98	7.47	5.20	4.54	5.83	8.29	6.09
	Passive							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	31.13	25.46	49.75	37.49	25.58	20.38	38.69	20.39
SE	4.79	5.49	6.77	5.90	5.31	6.44	7.51	6.91

Table 4. 6.

Variable error for children (means and standard errors in millimetres).

	Active							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	26.47	21.60	20.51	33.23	23.01	19.27	33.72	20.06
SE	5.91	5.97	5.85	6.67	6.56	7.01	6.49	7.82
	Passive							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
Mean	26.78	7.71	26.12	31.18	16.37	16.26	36.55	14.23
SE	5.09	3.21	5.92	6.93	5.65	3.76	6.57	8.12

4.3.1 *H1: Absolute and variable error will be higher in the passive condition.*

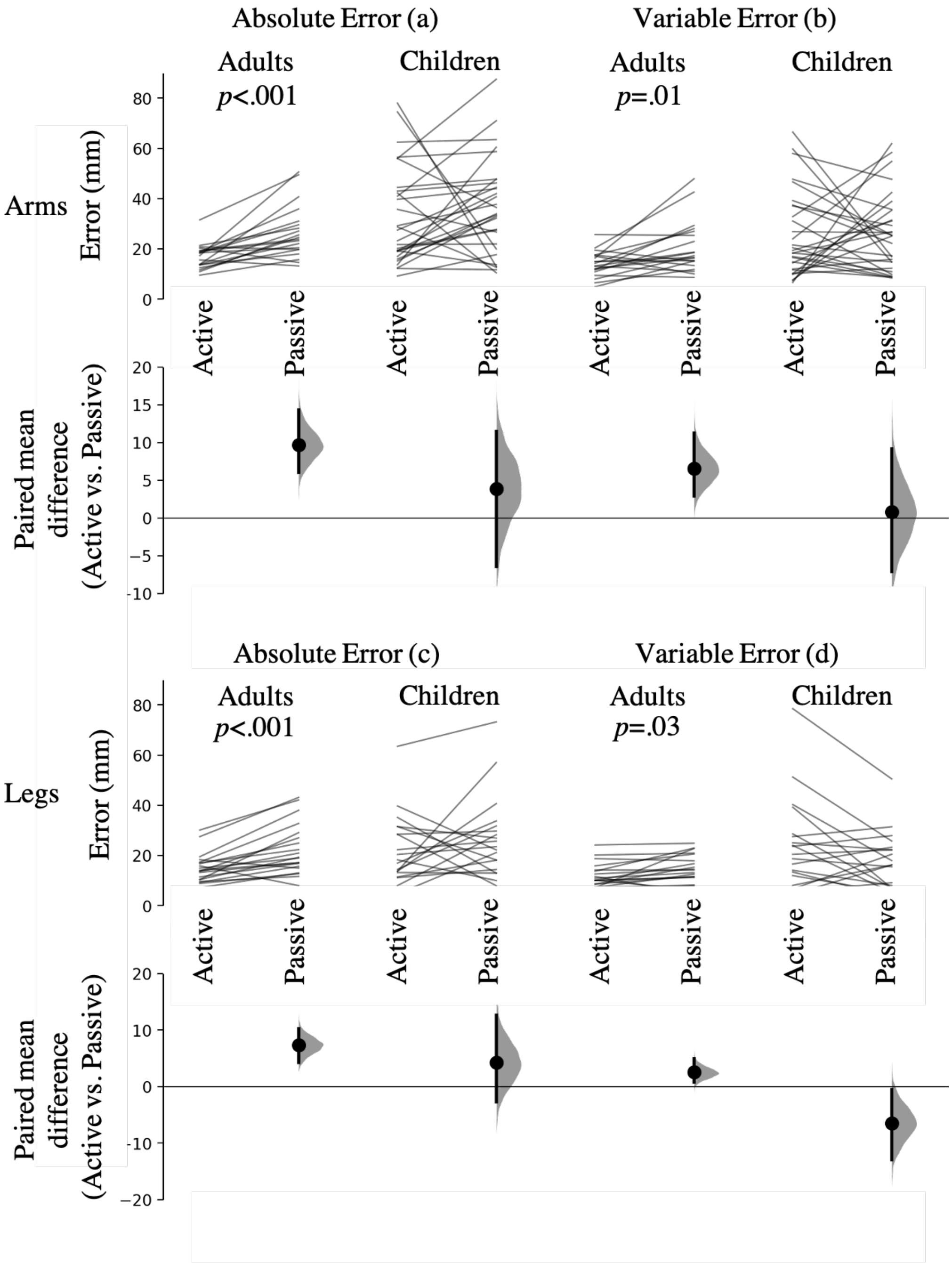

Figure 4. 2. Error in the active and passive conditions for adults and children. Subplots show each individual participant as a separate line. The paired mean difference (active vs. passive) is plotted on floating axes as a bootstrap sampling distribution with paired mean difference as a black dot, 95% confidence interval around mean difference as vertical error bars, and distribution of differences scores as shaded area. Data is presented as follows: absolute error for the arms (a), variable error for the arms (b), absolute error for the legs (c) and variable error for the legs (d). Y axes scales are not the same – they are designed to highlight significant effects for the reader. Plots created using resources from (Ho,

Tumkaya, Aryal, Choi, & Claridge-Chang, 2019). Significant main effects of movement type (with *p* values) are noted where relevant.

For children, H1 was not supported. There was no effect of movement type on absolute error for the arms, $F(1, 27)=0.55$, $p=.47$, $\eta p^2=0.02$, 90% *CI* [0.00, 0.16] (Figure 4. 2a) or the legs, $F(1, 17)=0.91$, $p=.35$, $\eta p^2=0.05$, 90% *CI* [0.00, 0.26] (Figure 4. 2c). There was no effect of movement type on children's variable error for the arms, $F(1, 27)=0.02$, $p=.90$, $\eta p^2<0.01$, 90% *CI* [0.00, 0.04] (Figure 4. 2b) or the legs, $F(1, 17)=3.35$, $p=.09$, $\eta p^2=0.17$, 90% *CI* [0.00, 0.40] (Figure 4. 2d).

Since testing H1 was our primary aim, we conducted additional Bayesian analyses to indicate the likelihood of the experimental hypothesis (that error would be higher in the passive condition) compared to the null hypothesis (that error would be similar in the active and passive conditions). We used the default parameters of a Bayesian repeated measures ANOVA in JASP software to obtain BF_{10}. We calculated BF_{01} using $1/BF_{10}$. Positive BF_{01} values indicate that the null hypothesis is more likely than the experimental hypothesis (Jarosz & Wiley, 2014). In the children's data, we found that the null hypothesis was more likely than the experimental hypothesis for absolute error (arms: $BF_{01}=33.33$; legs: $BF_{01}=4.17$) and variable error (arms: $BF_{01}=5.00$; legs: $BF_{01}=8.33$).

For adults, H1 was supported. Adults showed significantly higher absolute error in the passive condition (*M*=26.70mm, *SE*=2.36mm) than in the active condition (*M*=17.00mm, *SE*=1.10mm) for the arms, $F(1, 19)=20.98$, $p<.001$, $\eta p^2=0.53$, 90% *CI* [0.23, 0.67] (Figure 4.2a). Adults also showed significantly higher absolute error for the legs in the passive condition (*M*=22.33mm, *SE*=2.27mm) than the active condition (*M*=15.01mm, *SE*=1.31mm), $F(1, 19)=23.03$, $p<.001$, $\eta p^2=0.55$, 90% *CI* [0.25, 0.69] (Figure 4.2c). For the arms, adults showed significantly higher variable error in the passive condition (*M*=20.59mm, *SE*=2.32mm) than the active condition (*M*=14.06mm, *SE*=1.11mm), $F(1, 19)=9.20$, $p=.01$, $\eta p^2=0.33$, 90% *CI* [0.06, 0.53] (Figure 4.2b). Adults also showed significantly higher variable error for the legs in the passive condition (*M*=14.33mm, *SE*=1.33mm) than the active condition (*M*=11.78mm, *SE*=1.09mm) $F(1, 19)=5.75$, $p=.03$, $\eta p^2=0.23$, 90% *CI* [0.02, 0.45] (Figure 4.2d).

4.3.2 H2: Absolute and variable error will: a) be higher among children than adults, and b) reduce with age in childhood

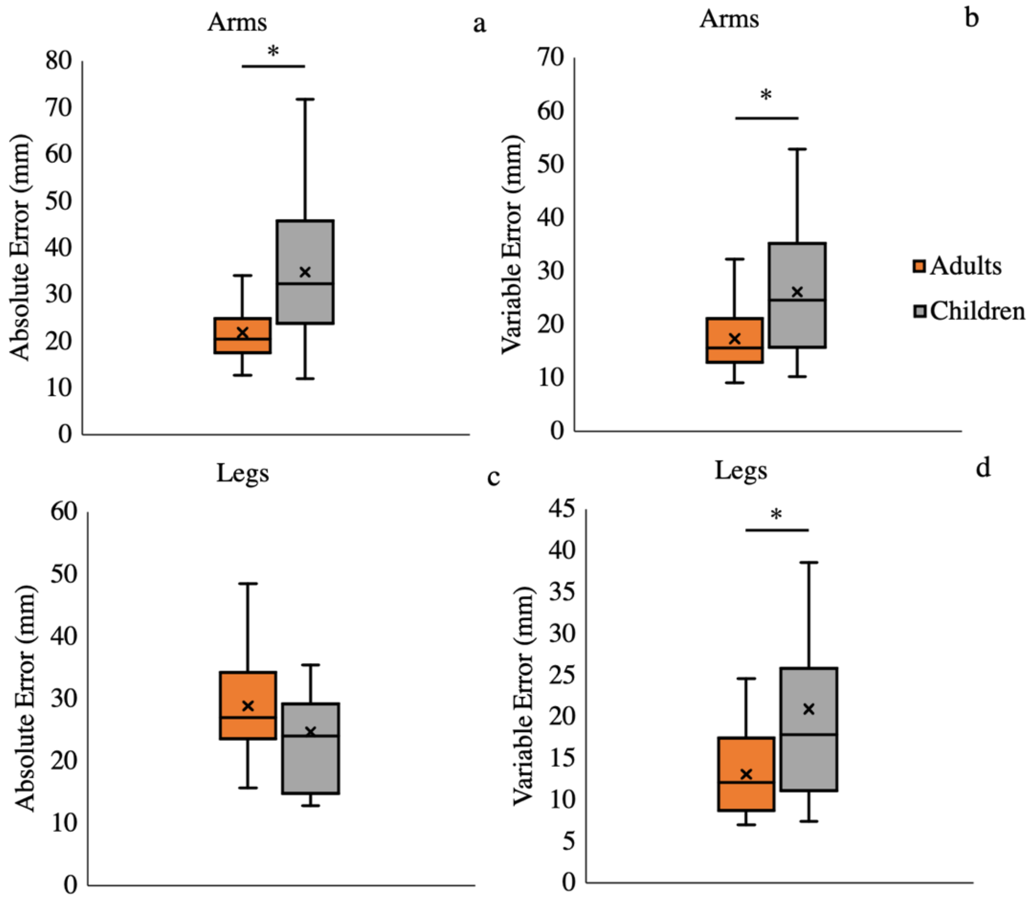

Figure 4. 3 Error for adults and children. Each boxplot shows the inter-quartile range, and whiskers extend to the minimum and maximum data points. Horizontal line marks the median and cross marks the mean. Subplots show: absolute error for the arms (a), variable error for the arms (b), absolute error for the legs (c), variable error for the legs (d). Y axes scales are not the same – they are designed to highlight significant effects for the reader. Significant differences between children and adults are indicated by asterisks.

H2a was supported. Children's absolute and variable error were higher than those of adults. For the arms, absolute error for children was significantly higher (M=34.80mm, SE=2.23mm) than for adults (M=21.85mm, SE= 1.47mm), U=123.50, p<.01, r = -0.48, 95% CI [0.24, 0.68] (Figure 4.3a). Children's variable error for the arms (M=26.07mm, SE= 2.17mm) was also significantly higher than that for adults (M=17.32mm, SE = 1.43mm), U=156.00, p=.01, r =-0.39, 95% CI [0.11, 0.63] (Figure 4.3b). For the legs, there was no significant difference in absolute error between children and adults, U=123.00, p=.06, r =-0.30, 95% CI [-0.02, 0.58] (Figure 4.3c). However, children's variable error for the legs (*M*=20.92mm, *SE*= 2.31mm) was significantly higher than adults' variable error (*M*=13.05mm, SE=1.06mm), *U*=111.00, *p*=.03, *r* =-0.35, 95% *CI* [0.06, 0.63] (Figure 4.3d).

In contrast, H2b was not supported. Because of this null result, we report Bayesian statistics here to aid interpretation. Among children, there was no effect of age on absolute error for the arms, *F*(1, 26)=0.74, *p*=.40, ηp^2=0.03, 90% *CI* [0.00, 0.18], BF_{01}=26.32 or the legs, *F*(1, 16)=0.02, *p*=.88, ηp^2=<0.01, 90% *CI* [0.00, 0.09], BF_{01}=5.08. There was no effect of children's age on variable error for the arms, *F*(1, 26)=2.49, *p*=.13, ηp^2=0.09, 90% *CI* [0.00, 0.27], BF_{01}=2.01 or the legs, *F*(1, 16)=0.97, *p*=.34, ηp^2=0.06, 90% *CI* [0.00, 0.28], BF_{01}=14.29.

4.3.3 H3: Movement type, distance and dominance will interact, such that absolute error is highest in the passive condition, at large distances, for the dominant arm.

For children, H3 was not supported. We did not find a significant three way interaction between movement type, distance and dominance on absolute error for the arms, *F*(1, 26)=0.15, *p*=.70, ηp^2=0.01, 90% *CI* [0.00, 0.12].

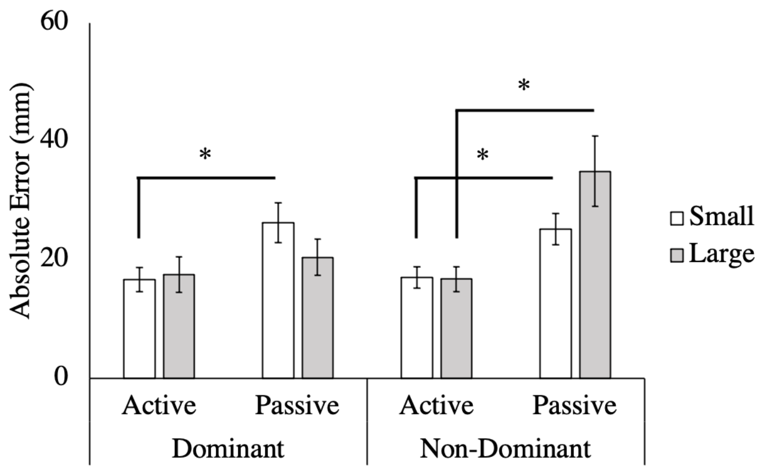

Figure 4. 4. Absolute error for the arms in adults. Plot shows mean values and standard errors for both the dominant and non-dominant arm, in the active and passive condition. Significant differences between conditions are indicated by asterisks.

For adults, H3 was partially supported. For adults, we found a significant three way interaction between movement type, distance and dominance on absolute error when completing the task with the arms, *F*(1, 19)=12.37, *p*<.01, ηp^2=0.39, 90% *CI* [0.11, 0.58] (Figure 4.4). However, this interaction was slightly different to what we expected. Bonferroni corrected post-hoc tests showed that, for small distances, adults' absolute error was significantly higher for the dominant arm in the passive condition (*M*=26.27mm, *SE*=3.38mm) compared to the active condition (*M*=16.68mm, *SE*=2.04mm), *p*<.01. At small distances, for the non-dominant arm, error was significantly higher in the passive condition (*M*=25.17mm, *SE*=2.67mm) than the active condition (*M*=17.06mm, *SE*=1.80mm), $p<.01$. For large distances, adults' absolute error was significantly higher for the non-dominant arm in the passive condition (*M*=34.92mm, *SE*=5.93mm) than in the active condition (*M*=16.76mm, *SE*=2.13mm), $p<.01$. At large distances, there was no effect of movement type for the dominant arm, $p=.173$. For the legs, adults did not show an interaction between movement type, distance and dominance, $F(1, 19)=0.44$, $p=.52$, $\eta p^2=0.02$, 90% *CI* [0.00, 0.20].

4.3.4 Additional Findings – Children

Among children there were a number of significant main effects of distance on error which we had not specifically predicted. For the arms, children showed significantly higher absolute error for large distances (*M*=40.31mm, *SE*=4.25mm) than small distances (*M*=28.96mm, *SE*=2.19mm), $F(1, 27)=9.46$, $p=.01$, $\eta p^2=0.26$, 90% *CI* [0.05, 0.45]. For the legs, children also showed significantly higher absolute error for large distances (*M*=27.65mm, *SE*=3.01mm) than for small distances (*M*=20.42mm, *SE*=3.49mm), $F(1, 17)=4.18$, $p=.04$, $\eta p^2=0.22$, 90% *CI* [0.00, 0.43]. For variable error, children also showed significantly higher error for the legs at large distances (*M*=24.68mm, *SE*=4.67mm) compared to small distances (*M*=16.21mm, *SE*=2.39mm), $F(1, 17)=4.60$, $p=.047$, $\eta p^2=0.21$, 90% *CI* [0.00, 0.44].

Distance also interacted with dominance in children but in different ways for the arms vs. the legs. There was an interaction between distance and dominance on children's variable error for both the arms, $F(1, 26)=4.48$, $p=.04$, $\eta p^2=0.15$, 90% *CI* [0.00, 0.34] and the legs, $F(1, 16)=5.85$, $p=.03$, $\eta p^2=0.27$, 90% *CI* [0.17, 0.49]. Bonferroni corrected post-hoc tests showed that, for the dominant arm, there was no significant effect of distance, $p=.58$. For the non-dominant arm, children's variable error was significantly higher at large distances (*M*=35.03mm, *SE*=4.51mm) than small distances (*M*=23.4mm, *SE*=4.1mm), $p=.03$. For the legs, the pattern was reversed. For the non-dominant leg, there was no significant effect of distance, $p=.88$. For the dominant leg, children's variable error was significantly higher at large distances (*M*=17.7mm, *SE*=3.7mm) than small distances (*M*=14.7mm, *SE*=3.2mm) $p<.01$.

4.3.5 Additional Findings - Adults

Among adults, we found unexpected effects of distance and an interaction between dominance and movement type. With the legs, adults showed significantly higher absolute error at short distances (*M*=20.09mm, *SE*=2.09mm) than long distances (*M*=17.25mm, *SE*=1.49mm) $F(1, 19)=4.43$, $p=.05$, $\eta p^2=0.19$, 90% *CI* [0.00, 0.41]. With the arms, there was an interaction between movement type and dominance on absolute error $F(1\ 19)=6.82$, $p=.02$, $\eta p^2=0.26$, 90% *CI* [0.03, 0.48]. For the dominant arm, absolute error was significantly higher in the passive condition (*M*=23.35mm, *SE*=2.22mm) than the active condition (*M*=17.1mm, *SE*=1.78mm), *p*=.01. For the non-dominant arm, absolute error was also significantly higher in the passive condition (*M*=30.04mm, *SE*=3.37mm) than the active condition (*M*=16.91mm, *SE*=1.28mm), *p*<.001. However, the effect of movement type for the non-dominant arm was much larger than that for the dominant arm.

4.4 Discussion

Previous developmental work has not disentangled the relative contributions of feedforward and feedback proprioceptive cues to children's awareness of limb position. We investigated the extent to which children (4- to 13-years) benefit from forward models on a memory-based proprioceptive task by asking participants to actively reproduce specific movements following active or passive target movement. We found no evidence of children benefitting from forward models for proprioceptive memory. Further, children's performance did not improve with age, was poorer for larger movement distances, and was affected by limb dominance in different ways to adults' performance.

4.4.1 Limited Use of Forward Models Among Children

As hypothesised (H1), adults reproduced movements more accurately and with lower variability following active target movement. This result was not explained by variations in movement time during the active condition (Appendix 2). Our findings among adults align with previous research (Adamovich et al., 1998; Coslett et al., 2008; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Gritsenko et al., 2007; Laufer et al., 2001). We interpret this as adults benefitting from forward models generated during active movement for memory-based proprioceptive judgements. Specifically, in the active condition, adults can use discrepancies between actual and predicted sensory information during the target phase to refine their forward model (Wolpert & Flanagan, 2001). A better-refined forward model subsequently benefits movement accuracy in the report phase.

We expected that children would also benefit from forward models for accuracy and variability. However, in the present study, children's accuracy and variability were not significantly different in the active (forward model available) and passive (no forward model) conditions. Our Bayesian analysis showed that the null hypothesis (no effect of movement type) was more likely than the experimental hypothesis (H1). This supports no significant effect of movement type on children's error. Based on this result, we cannot be sure whether i) children do not generate forward models for active movement or ii) children generate forward models but do not benefit from them for memory-based proprioceptive judgments. Even if children do generate forward models, they may be unable to effectively integrate them with sensory feedback (Gori, Del Viva, Sandini, & Burr, 2008; Nardini et al., 2008). There is a further possibility: that children generate noisy, poorly-refined forward models. However, this would likely produce poorer performance in the active condition, as per Gori et al (2012). Whatever the mechanism, our data show that children did not benefit from forward models for this memory-based proprioceptive task. This contrasts with previous studies using non-memory proprioceptive tasks, like sensorimotor adaptation (Deng et al., 2019; Kagerer & Clark, 2014) and speed-based tasks (Van Roon et al., 2008; Wilson & Hyde, 2013) interpreting adaptation after-effects and rapid movement updating as developing forward model use in children.

Our data suggest that the improvements in upper-limb proprioception reported for other tasks (Contreras-Vidal, 2006; Holst-Wolf et al., 2016; Sigmundsson et al., 2000; von Hoftsen & Rösblad, 1988) could be driven by improving use of sensory feedback. Indeed, children do rely on proprioceptive sensory feedback to control their movements, showing greater error when this feedback is experimentally disrupted (Hay & Redon, 1997; Hay et al., 2005). Children may need to first develop good sensory feedback mechanisms, before they can generate accurate forward models. Forward models require reliable sensory feedback in order to be formed, updated and improved - sensory feedback must be compared with predictions so that the model can learn from errors (Wolpert & Flanagan, 2001). Children may not yet have sufficiently reliable sensory feedback mechanisms to facilitate effective forward models.

4.4.2 No Improvement Across Childhood

As per previous work (Goble et al., 2005; Holst-Wolf et al., 2016), our data suggest that proprioception remains immature in late childhood/early adolescence. We can speculate about a number of reasons why proprioception might take so long to mature. Firstly, *neurophysiological factors*: for example, muscle spindle sensitivity continues developing until at least 11 years (Grosset, Mora, Lambertz, & Perot, 2007; Holst-Wolf et al., 2016). Secondly, *motor imagery*: imagined movements are an internal model of movement (Crammond, 1997). They follow the same temporal constraints as executed movements, and the correlation between actual and imagined movement time continues to strengthen from childhood, through adolescence, and into adulthood (Caeyenberghs, Wilson, Van Roon, Swinnen, & Smits-Engelsman, 2009; Choudhury, Charman, Bird, & Blakemore, 2007a, 2007b). Finally, *executive functions*: working memory and attention continue maturing into adolescence (Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Blakemore & Choudhury, 2006). This could make remembering limb movements challenging in childhood, when attention and working memory are immature. Together, these factors could explain why both our work and previous work (Goble et al., 2005; Holst-Wolf et al., 2016) have found that performance on proprioceptive tasks remains immature in late childhood/early adolescence.

However, contrary to other literature (Sigmundsson et al., 2000; von Hoftsen & Rösblad, 1988), and contrary to our hypothesis (H2), we did not find any improvements during childhood. Different proprioceptive tasks have very different requirements which may explain the different developmental profiles. For example, Sigmundsson et al (2000) and von Hoftsen and Rösblad (1988) asked participants to point to their own body parts without being able to visually locate them. On this task, performance improved rapidly from early to mid-childhood. In contrast, we asked participants to remember and reproduce linear limb movements and found no improvements between 4 and 13 years. Similarly, Hay and Redon (1997) found no improvements between 5 and 11 years in in children's ability to point to visual targets using only proprioceptive information (vision of the arm was occluded). It may be more challenging for children to remember and recreate the movement of a single limb (as per our task), than it is to proprioceptively locate their own body parts without memory demands (as per Sigmundsson et al., 2000; von Hoftsen & Rösblad, 1988). This might explain why we found that children's performance was immature at all ages on a memory-based proprioceptive task. Further, children's performance may have changed with age in other ways which we did not measure (e.g. in movement smoothness).

4.4.3 Larger Error for Larger Movements

For both the arms and legs, children were less accurate over larger distances. For the legs, children were also more variable over large distances**.** There are a number of reasons why children might show higher error for larger movements. Firstly, *accumulating error*: a larger movement presents greater potential for sensory error to accumulate. Secondly, *kinematic priors*: the brain might predict likely limb states using kinematic priors (most frequently experienced limb states) close to the body (Gritsenko et al., 2007; Howard, Ingram, Kording & Wolpert, 2009; Wilson, Wong, & Gribble, 2010). Adult research (Wilson et al, 2010) shows that proprioceptive judgements are more accurate when the effector is closer to the body. Thirdly, *attention*: larger movements take longer, and therefore, might be more demanding on working memory and attention. Finally, *surprise*: smaller movements might have been more surprising (and more memorable) than larger movements. The longer the movement progresses, the more expected the target position becomes (Gritsenko et al., 2007). However, none of these potential mechanisms explain why adults did not show the same consistent overshooting as children.

4.4.4 Different Effects of Dominance for Children and Adults.

Beyond simple main effects of movement distance, we also found interactions between distance, movement type and dominance. Previous work has shown that following passive target movement, error is higher for the *dominant arm*, especially for larger movements (Goble et al., 2005, 2006, 2009). As expected (H3), we also found interactions between distance, dominance and movement type.

Adults showed no dominance effects for the legs. At small distances, adults showed higher absolute error in the passive condition for both the dominant and non-dominant arms. However, at large distances, adults showed higher absolute error in the passive condition for the *non-dominant arm* only. Further, the effect of movement type on absolute error was much larger for the *non-dominant arm*. In summary, proprioception in the *non-dominant arm* is most vulnerable to the removal of a forward model (in the passive condition). This effect is more pronounced at larger distances, when there is more potential to accumulate error. Similarly, for children the *non-dominant* arm showed significantly higher variable error at large distances. These results contrast with those of Goble et al who find that proprioceptive accuracy is poorest in the *dominant arm* (Goble et al., 2005, 2006, 2009). In contrast, children's variable error for the *dominant leg* only was significantly higher at large distances. This aligns with Goble et al.'s findings in upper limb tasks (Goble et al., 2005, 2006, 2009) – that the *dominant limb* tends to perform more poorly.

Why might our results contrast with those of Goble et al (2005, 2006, 2009)? Goble et al. asked participants to report a target elbow angle (always specified passively) with the same or contralateral limb. In contrast, we asked participants to report linear target movements (specified actively or passively) with the same limb only. These methodological differences might contribute to the disparity in results. Nonetheless, both sets of results, and those of other studies (Chokron, Colliot, Atzeni, Bartolomeo, & Ohlmann, 2004; Schmidt et al., 2013) show that dominance has an impact on proprioceptive performance. This is an important finding since other tasks which have manipulated movement type (active/passive), have not measured effects of limb dominance (Adamovich et al., 1998; Erickson & Karduna, 2012; Fuentes & Bastian, 2010; Laufer et al., 2001). Also important is that dominance affected performance differently in adults vs. children. This is surprising given that handedness can be observed very early in infancy, and is somewhat stable in toddlerhood (Nelson, Campbell, & Michel, 2013)

4.4.5 Limitations and Future Directions

There are several additional measures which would make for a stronger methodology in future studies. Firstly, we did not measure muscle activity, force, or movement acceleration. This presents some challenges for interpreting our findings. We cannot determine whether participants exerted muscle force even in the passive condition. This may have contributed to the lack of difference between active and passive condition performance in children. We also cannot be sure what type of movements participants were making. Movements in the active condition may have been ballistic and forceful with participants relying on the physical stopper to end the movement in the target phase. In the report phase, movements may have been more controlled with a bell-shaped acceleration profile whereby participants decelerated toward their perceived target position. There could also have been variations in the acceleration and force profile of movements across conditions (active vs passive) and across participants. As well as recording muscle activity, force, and acceleration, researchers in future studies should also consider using an auditory tone to signal target location in the target phase rather than a physical stopper. This might encourage participants to make more steady, controlled movements since they would not be able to rely on the stopper to end their movement. This might help to ensure comparable movements in the target and report phases, across active and passive conditions, and between participants.

Secondly, there was a delay between the target phase and the report phase, during which the experimenter removed the stopper (in the active condition) and gave instructions. Unfortunately, we did not record the length of this inter-phase delay and variation in the length of this delay could have an impact on proprioceptive memory in the report phase. Thirdly, we cannot be sure whether children's performance on our task was poorer than adults' because i) children had poorer proprioceptive memory than adults, or ii) children had poorer proprioception per se. To address this, future work should include a measure of proprioceptive acuity which is not reliant on memory, for example limb position matching as used by Sigmundsson et al (2000) or von Hoftsen and Rösblad (1988).

The present study may also be limited in terms of implications for real behaviour, since where we did find significant differences, the magnitude of these was small. For example, among adults the difference in absolute error between the active and passive condition was less than 1 centimetre. It is questionable whether such small differences would have a meaningful impact on everyday movement.

4.5 Conclusions

Participants made active (self-generated) or passive (equipment generated) target movements. They then reproduced these movements actively from memory. In the active condition, adults showed lower absolute and variable error for arm and leg movements. In contrast, children's accuracy and variability were no better in the active condition than the passive. Therefore, we found no evidence that children benefit from forward models for memory-based proprioceptive judgements. In our task, children's performance did not improve between 4 and 13 years. Children's performance was significantly poorer than adults, was poorer when reporting larger movements, and was affected by limb dominance (although in different ways to adults' performance). We argue that children are predominantly reliant on sensory feedback for proprioceptive memory, rather than on feedforward mechanisms. Future work should establish whether i) children do not generate forward models or ii) children struggle to integrate feedforward and feedback cues for memory-based proprioceptive tasks.

4.6 From Single-Limb to Whole-Body Proprioception

In study 3, we asked whether or not children benefit from forward models for proprioceptive memory. We compared children's ability to remember and reproduce movements following active or passive target movement. We found that performance was similar in the active and passive conditions, suggesting that children do not benefit from forward models like adults. Rather, children solve the task using only sensory feedback. This also suggests that childhood improvements in proprioception reported in previous studies (Contreras-Vidal, 2006; Holst-Wolf et al., 2016; Sigmundsson et al., 2000; von Hoftsen & Rösblad, 1988) might rely predominantly on improving use of sensory feedback. Further, in our sample (4- to 14-years) children's error was overall higher than adults', suggesting that proprioception does not mature until at least adolescence. This concurs with previous research, showing continued refinement of proprioception into adolescence (Goble et al., 2005; Holst-Wolf et al., 2016). However, it also highlights that, for children, even remembering and reproducing single limb positions is challenging.

In many everyday activities (like getting dressed or playing a sport) the whole body must be coordinated into complex configurations. Crucially, we must remember these complex whole-body configurations and recreate them when we next attempt the activity. We can assume that whole-body proprioception must be extremely challenging for young children. Therefore, it would be beneficial to find activities which allow children to practice and improve their whole-body proprioception. This was the motivation for study 4.

In study 4, we evaluated the effects of a school-based creative dance program on children's whole-body proprioception. In collaboration with Bare Toed Dance Company, we delivered 6 weekly dance sessions. The sessions were specifically tailored to train children's proprioceptive awareness. We measured whole-body proprioception and general movement skills (manual dexterity, throwing and balance) before and after the intervention. We compared the dance intervention with a non-creative, standard physical activity program, and a non-movement control program. We expected that the tailored dance program would improve proprioception to a greater extent than standard physical activity.

We chose dance as the training method since research shows superior proprioception among professional dancers compared to controls (Jola et al., 2011; Kiefer et al., 2013). Other more recent work has also shown that dance sessions can improve single limb proprioception among pre-schoolers (Chatzopoulos, 2019; Chatzopoulos et al., 2018). Further, dance sessions can be easily and cheaply delivered within the school day as part of the normal PE provision. This makes dance more suitable for training children than other proprioceptive training programs. These are usually targeted to specific body parts, injuries or disease-related deficits (Aman, Elangovan, Yeh, & Konczak, 2015). These training programs can be too specific for general proprioceptive development and, due to their repetitive nature, are unlikely to engage children effectively. Further, simple, repetitive interventions do not provide children with varied motor experience, which is crucial for motor development and learning (Adolph et al., 2018; Lee, Cole, Golenia, & Adolph, 2018; Ossmy et al., 2018).

In summary, study 3 showed us that across childhood (4- to 14-years), proprioception remains immature, even for simple, single limb movements. Proprioception is a crucial sensorimotor skill at the core of many daily activities. Further, most daily activities require multi-limb, or whole-body coordination. Therefore, in study 4 we sought to improve children's whole-body proprioception through dance training.

Chapter 5

Study 4 - Can Dance Improve Children's Proprioception?

5.1 Introduction

Most daily activity requires coordinating the whole body into complex positions using proprioception. Being able to sense limb position is also crucial for accurate movement control. Patients with proprioceptive loss experience debilitating motor deficits, such as unstable gait, poor balance, fine motor difficulties, difficulties detecting touch, and distorted movement trajectories (Sainburg et al., 1993). Even in healthy individuals, when proprioception is disrupted via tendon vibration, both adults and children show systematic movement errors (Hay & Redon, 1997). As children learn new motor skills (like getting dressed or playing a sport) they must use proprioceptive cues from the body to remember and reproduce complex, whole-body positions. Despite being crucial for daily activities, children perform poorly at even simple proprioceptive judgements (Contreras-Vidal, 2006; Goble et al., 2005; von Hoftsen & Rösblad, 1988; Study 3). In this introduction, we discuss the development of proprioception and the potential to improve proprioception through dance training. We then introduce the present study, in which we sought to improve complex, whole-body proprioception using a school-based dance intervention for 5- to 6-year-olds.

5.1.1 The Development of Proprioception

Young children (5- to 6-years) perform relatively poorly on a range of proprioceptive tasks. When drawing to visual targets without vision of the hand, 6-year-olds perform with more than twice as much error as 10-year-olds (Contreras-Vidal, 2006). When children point to their own finger using the contralateral hand without vision, random error is 36% larger at 5 years compared to at 8 years (von Hoftsen & Rösblad, 1988). Beyond mid-childhood, proprioception remains immature even into adolescence. Goble et al (2005) asked children (8- to 10-years) and adolescents (16- to 18-years) to reproduce target elbow angles whilst blindfolded. Children's absolute error was over 1.5 times greater than that of adolescents. Using the same paradigm, Holst-Wolf et al (2016) found that even adolescents performed the task more variably than adults. In summary, proprioception has a very protracted developmental profile: it is poor in early childhood and remains immature even in adolescence. However, all of the above-described studies used relatively simple tasks. None of these tasks required proprioceptive judgements to be made with all four limbs simultaneously. Performance on more complex, whole-body tasks (reflective of everyday movement demands) might be even poorer among children and take even longer to mature.

Given how important proprioception is for the control of movement (Sainburg et al., 1993), it would be beneficial to boost its development in young children. The 5- to 6-year age range may represent a particularly malleable period in proprioceptive development, suitable for intervention. At this age, studies have reported that proprioception is immature but improving rapidly (Contreras-Vidal, 2006; von Hoftsen & Rösblad, 1988). It is important for interventions to be introduced during times of developmental change and variability. At these times, the developing system might be influenced by training (Thelen, 1995).

5.1.2 Training Proprioception

Proprioception can be trained in many different ways, such as balance training, robot-assisted passive movement, joint position matching, and vibration therapies (Aman et al., 2015). However, these types of intervention are simple, repetitive, and unlikely to engage children. Many of these interventions are also not suitable for delivery at home or school. Further, these simple, repetitive interventions do not align with children's need for varied motor practice when learning new skills (Adolph et al., 2018). When motor experience is less varied, motor learning is poorer (Lee et al., 2017; Ossmy et al., 2018). Dance training could provide a varied and engaging means of training children's proprioception.

A number of different dance styles can have a positive impact on general movement skills. Greek dance training, twice weekly for twenty weeks improved performance on a broad motor assessment battery among 4- to 6-year-olds (Venetsanou & Kambas, 2004). Thirty six weeks of modern dance choreography training improved both motor skills (e.g. running and jumping) and fitness (e.g. push ups and sit ups) among 5- to 14-year-olds (Ross & Butterfield, 1989). For 4- to 6-year-olds, locomotor skills (e.g. galloping, jumping, leaping and skipping) can be improved through music and movement percussion sessions (Derri, Tsapakidou, Zachopoulou, & Kioumourtzoglou, 2001). These studies demonstrate the benefits of dance and creative movement for a broad range of gross motor outcomes. These gross motor skills are underpinned by more low-level sensorimotor factors like proprioception. Could dance interventions be used to specifically improve proprioception?

Among expert dancers, proprioception is superior to that of non-dancers. Professional dancers show fewer platform oscillations when balancing on an unstable surface compared to non-dancers (Golomer et al., 1999). Dancers are also less influenced by a tilted visual landmark when asked to hold a rod at a vertical angle (Golomer et al., 1999). Expert ballet/contemporary dancers can point to the location of their finger with the contralateral hand whilst blindfolded more accurately than non-dancer controls (Jola et al., 2011). Professional ballet dancers can also remember and recreate target ankle, knee, and hip angles more accurately than non-dance controls (Kiefer et al., 2013). Together, these studies suggest that dancers have superior proprioception. However, we cannot be sure whether dance experience improves proprioception or whether those with superior proprioception excel at dance. By looking at training studies in children, we can more clearly see whether dance experience can improve proprioception.

Chatzopoulos (2019) measured proprioception in 7-year-olds before and after three months of twice weekly ballet training. Proprioception was measured by the experimenter moving the knee to a target angle. The participant then had to actively recreate the target angle. Before the intervention, the ballet group had similar proprioception to a control group who received physical education (PE) as usual. After the intervention, the ballet group had significantly better proprioception than controls. Other forms of dance can also be beneficial for children's proprioception. In another study by Chatzopoulos et al (2018), pre-schoolers received 8 weeks of bi-weekly creative dance sessions. Following this, knee joint proprioception was significantly improved relative to a control group who engaged in only unstructured free-play. This study provides promising evidence that creative dance training can enhance children's proprioception.

However, all of these studies with both professional dancers (Jola et al., 2011; Kiefer et al., 2013) and children (Chatzopoulos, 2019; Chatzopoulos et al., 2018) used only single limb tasks. These simple tasks have provided clear evidence that dance experience is associated with better proprioception. Nonetheless, single limb tasks might overestimate the abilities of children, since most naturalistic action is more complex and requires whole-body control. Training whole-body proprioception would be a more ecologically useful aim for dance intervention.

5.1.3 The Present Study

In designing a dance intervention, we must also consider the practical issues associated with implementing a children's training program. Schools have limited time and resources, which can impact on the successful implementation of children's physical activity programs (Naylor et al., 2015). As such, a feasible training program should be low cost and easy to include within the existing school timetable. Therefore, in the present study we introduced a physical activity program that did not require any extra resources or equipment and did not take up too much time during the school day. We measured the effect of weekly creative dance sessions, over six weeks, specifically tailored to improve children's whole-body proprioception. We worked with 5- to 6-year-olds, for whom proprioception is poor, but developing rapidly (Contreras-Vidal, 2006; von Hoftsen & Rösblad, 1988). We included two control groups. One control group received general, non-creative PE sessions and were included to indicate whether creative dance has benefits above and beyond those of general physical activity. A second control group learned spoken French and were included to control for any confounding effects of general engagement in novel activities and interaction with the unfamiliar experimenter. We measured whole-body proprioception (remembering and reproducing whole-body configurations), basic movement skills (manual dexterity, throwing and balance), and enjoyment of physical activity before and after the intervention.

Previous studies found positive effects of dance on proprioception among both professional dancers (Golomer et al., 1999; Jola et al., 2011; Kiefer et al., 2013) and children (Chatzopoulos, 2019; Chatzopoulos et al., 2018). Therefore, our first hypothesis was that proprioception would improve to a greater extent for the dance group compared to the PE or French group (H1). We expected this particularly because our dance program was designed to specifically target proprioception. Our second hypothesis was that general movement skills would improve to a greater extent for the dance and PE groups compared to the French group (H2). This is because both dance (Derri et al., 2001; Ross & Butterfield, 1989; Venetsanou & Kambas, 2004) and general PE (Ericsson & Karlsson, 2014) engagement are associated with improved motor skills. These previous studies (Derri et al., 2001; Ross & Butterfield, 1989; Venetsanou & Kambas, 2004) trained motor skills more frequently/over a longer time scale than the present study. However, we were specifically interested in the potential of a feasible, low-investment intervention that UK schools might easily be able to adopt. Finally, since engagement in physical activity correlates positively with enjoyment of physical activity (Sallis, Taylor, Prochaska, Hill, & Geraci, 1999), we predicted that enjoyment of being active would increase for the PE and dance groups but not for the French group (H3).

5.2 Methods

5.2.1 Design

We used a mixed design. There was one between-subjects factor: intervention (three levels: dance, PE and French). Each school was randomly assigned to one of the three interventions. There was one within-subjects factor: time (two levels: before (time 1) and after (time 2) the intervention). We measured the following dependent variables at both time points: enjoyment of physical activity, general movement skills (using tasks from the MABC 2 (Henderson et al., 2007): manual dexterity, static balance, throwing), and finally our own measure of whole-body proprioception. In order to assess whether the samples from the different schools were broadly comparable, we also recorded receptive vocabulary score using BPVS III (Dunn et al., 2009) and any developmental disorders or diagnoses in the participant groups.

5.2.2 Participants

The study was approved by the Psychology Department Ethics Committee and carried out according to the principles laid down in the 1964 Declaration of Helsinki. Children were recruited from year one classes in three primary schools in north east England. All schools were rated as ‘Good’ by the Office for Standards in Education in 2018. The Index of Multiple Deprivation rank for each school’s post code were as follows: French (1,402), dance (22,280), PE (31,529), where 1 is the most deprived area in the UK and 32, 844 the least deprived (UK Government, 2019). We report this information as a proxy for socioeconomic status of the participants. Socioeconomic status can have an impact on both motor skills and language ability (McPhillips & Jordan-Black, 2007). Therefore, this information may be useful for interpreting our results.

At the start of the project: children in the dance group had mean age 5.5 years, *N*=12 (6 female), and mean BPVS standardised score of 96.7 (*SE*=4.53); children in the PE group had mean age 5.5 years, *N*=19 (8 female), and mean BPVS standardised score of 105.3 (*SE*=7.84); children in the French group had mean age 5.6 years, *N*=17 (7 female), and mean BPVS standardised score of 93.1 (*SE*=10.22). The BPVS scores were significantly different across groups $F(2, 42)=7.096$, $p=.002$. Bonferroni corrected post hoc tests showed that the PE group scored significantly higher than the French group $p=.002$. Date of birth was not provided for two children in the French group (therefore, we could not calculate BPVS scores for these children). In the dance group, one child was autistic and one child had neurofibromatosis. In the PE group, one child had a speech delay. No disorders or diagnoses were reported for the French group.

5.2.3 Procedures

Parents provided written informed consent and reported children's date of birth and any disorders/diagnoses. The study then proceeded in three stages: stage 1 – baseline, stage 2 – intervention, stage 3 – post-intervention.

5.2.3.1 Stage 1 – Baseline. Testing sessions were conducted in school. Children wore their school uniforms (shoes, polo shirt and jumper, with trousers or skirt/dress, and school shoes) which were easy to move in. Children wearing a skirt/dress also wore sports shorts underneath.

To measure verbal ability, we administered the BPVS III (Dunn et al., 2009).

To measure general movement skills for each child, we used the MABC 2 (Henderson, et al., 2007) Age Band 1 to measure: manual dexterity (Manual Dexterity 3, Drawing Trail), throwing (Aiming & Catching 2, Throwing Beanbag onto Mat), and balance (Balance 1 (Static), One-Leg Balance).

We measured enjoyment of being active using a 'smile-o-meter' (inspired by Van Dijk, Lingnau, & Kockelkorn, 2012). This included five faces ordered from sad to happy (1-5). To introduce children to the smile-o-meter and to ensure they understood the meaning of the five response options, we began by asking the children questions about food. We asked them to indicate how much they liked chocolate, mushrooms and carrots by first talking them through the five response options *("1. I do not like chocolate at all. 2. I don't like chocolate much. 3. Chocolate is ok. 4. I like chocolate a bit. 5. I really like chocolate a lot").* Children were then read the following: *"Being active means moving our bodies, having fun and keeping fit and healthy. Being active can mean playing sports, running and jumping, dancing or playing outdoors. How much do you like being active? ".* They were then asked to choose a smiley face corresponding to one of the following options: *"1. I do not like being active at all. 2. I don't like being active much. 3. Being active is ok. 4. I like being active a bit. 5. I really like being active a lot".* They responded verbally or by pointing using the smile-o-meter.

To measure proprioception, we used a 'target and report' style task, which was completed lying down on the floor to avoid additional balance demands. Children lay on the floor, face up. Under each limb we placed a protractor marked on a flat wooden board (Figure 5. 1). For the arms, we placed the protractor such that 0 degrees extended vertically upwards from the shoulder joint. When the arms were extended horizontally, they aligned with 90 degrees on the protractor. For the legs, we placed the protractor such that 0 degrees extended vertically downwards from the sit bone. Each of the four protractors was moveable and could be repositioned to accommodate children of varying size.

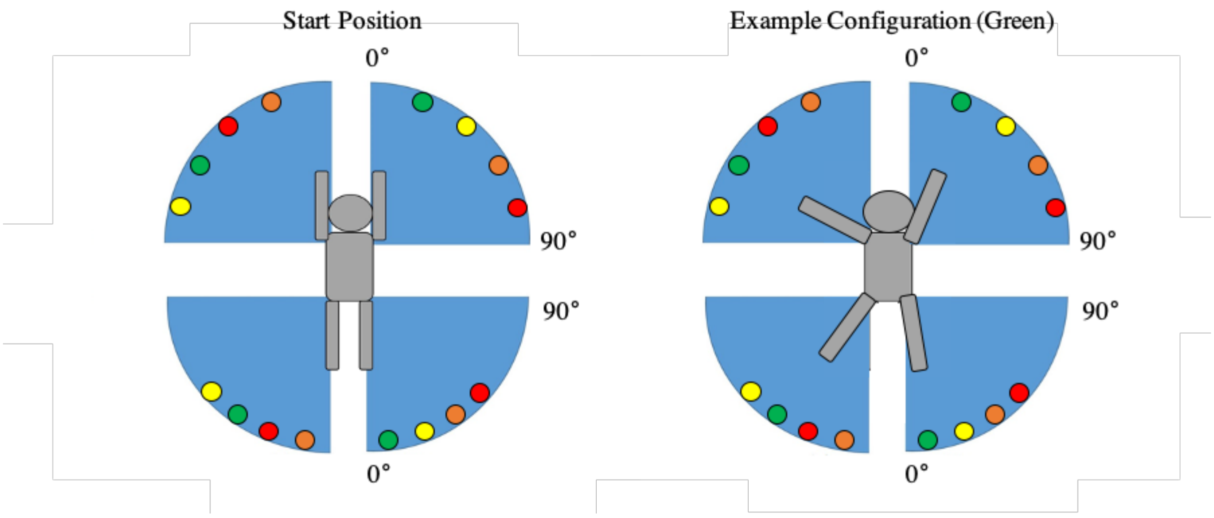

Figure 5. 1. Equipment set up.

There were four target position configurations. In each configuration, each limb was positioned at a different target angle from its start position. To help the experimenter locate the target angles, they were marked onto the protractors with small coloured stickers: one for each of the four target angles for each limb (green, yellow, orange and red – schematic representation given in Figure 5. 1). Target angles were distributed within a comfortable movement range for the arms and legs, this means that the target angles for the legs were smaller than those for the arms. No target positions were at the extremes of the movement range. The four configurations are described in Table 5. 1. The four configurations were presented in a random order to each child.

Table 5. 1.

Target Configurations.

Configuration	Left Arm Target Position (Degrees)	Right Arm Target Position (Degrees)	Left Leg Target Position (Degrees)	Right Leg Target Position (Degrees)
Green	15	55	8	24
Yellow	35	75	16	32
Orange	55	15	24	8
Red	75	35	32	16

The proprioception task was administered as follows with one practice trial and four recorded trials:

1. *"For this game, I am going to move your arms and legs into different positions. You have to try to remember exactly where I put your arms and legs. Then, after that, I'm going to ask you to put your arms and legs back to where I put them."*
2. *"Can you stretch your arms and legs out straight like a pencil?"*
    a. The experimenter stood in front of the child (by the child's feet) to also physically demonstrate the start position to the child. The experimenter continued once the child had their arms straight above their head and legs straight and together.
3. *"Now I am going to move your arms and legs"*
    a. The experimenter moved the child's arms and legs to the target angles in the following order: Left leg, right arm, right leg, left arm. The experimenter also recorded the time taken (to the nearest second) to position all four limbs.
4. *"Keep your arms and legs really still in the place where I put them"*
5. *"Now remember that position, remember exactly where your arms and legs are."*
6. *"And now go straight like a pencil."*
    a. The experimenter also physically demonstrated the start position to the child and continued once child was in the start position.
7. *"And now, can you move your arms and legs back to exactly the place where I put them?"*
    a. The experimenter recorded time taken to respond (to the nearest second) from the moment the child began moving their limbs until they were still.

8. Once child had moved into position: *"Now stay really still in that position, don't move and I am going to write down where you have put your arms and legs"*
    a. The experimenter recorded the child's responses by marking the location of each middle finger tip and the location of the centre of each heel. If necessary, the experimenter gently straightened the child's fingers or rotated the ankle upright (so that the centre of the heel was in contact with the protractor) to take the measurements.
9. *"Brilliant, well done! Now we are going to do that a few more times"*
10. Procedures were repeated from step 2 for the four trials.

The children had their eyes open throughout the proprioceptive task. Since the children were only 5 years old, this allowed them to follow physical, visual cues from the experimenter without having to rely solely on verbal instruction. Because the children were lying down and because the task involved the whole body it was not possible for children to solve the task using vision. They would not be able to accurately perceive and position all four limbs simultaneously using only visual feedback. Good performance demanded that they use proprioception.

5.2.3.2 Stage 2 – Intervention. All groups received activity sessions (dance, PE or French) for between 45mins and one hour per week, for six weeks. Sessions were incorporated into the normal school day. Dance sessions were delivered by an experienced dance teacher from a local dance company (Bare Toed Dance Company). The PE and French sessions were delivered by the lead researcher.

The French group learned basic French through verbal games, card sorting/matching, finding objects in the classroom, and worksheets which required them to glue words or letters onto paper. They did not do any movement beyond that required by normal classroom activities (e.g. sticking onto paper, arranging cards, opening envelopes, raising their hand). They did not use pens or pencils and they were not given any movement-related feedback. Each session lasted between 50 and 60 minutes.

The PE group began each session with a warm-up of simple stretches, walking and running on the spot, and jumping. The sessions then consisted of physical games designed to be strengthening and provide cardio exercise: team races (running, jumping, skipping, hopping, crawling), tag, circuits (squats, sit ups, plank, star jumps). The children were expected to attempt the correct movements and were given motivational feedback throughout (e.g. "keep going", "can you run faster?"). However, they were not given specific feedback on the quality of their movement. None of the activities focused on body shape or proprioception. Each session lasted between 45 and 50 mins (to fit with the school schedule and allowing time for children to change into PE kit).

The dance group engaged in free and creative movement to music, facilitated by a professional dance teacher from Bare Toed Dance Company. They played movement games, selected by the dance teacher to promote proprioception. This included: dancing freely to music, copying other people's body shapes, mirroring/copying others' movements, making shapes of different qualities (e.g. representing a firework, or a leaf), noticing and correcting differences in body shapes between self and other or between two others, sculpting a partner into a specific body position, pointing to a partner's finger with eyes closed. All of the activities emphasised creativity, encouraging the children to move their bodies in new and interesting ways. The focus was very much on becoming aware of and noticing the details of complex body positions. Each session lasted 40-45 mins (to fit with the school schedule and allowing time for children to change into PE kit).

5.2.3.3 Stage 3 – Post-intervention. After the six-week intervention, we administered the measures as per stage 1, but without the BPVS III (Dunn et al., 2009) since we did not expect this to change as a result of our intervention and wanted to keep testing time to a minimum.

5.2.4 Analysis

We calculated standardised scores from the tasks taken from the MABC 2 (Henderson, et al., 2007) and BPVS III (Dunn et al., 2009). For the proprioception task, error for each limb was measured in degrees as the difference between the target angle and the angle at which the participant placed their limb (see step 8a of the proprioception task procedures). We took the error value from each of the four limbs and averaged these to form a composite score for each of the four trials. We then calculated average error (degrees) for each participant across the four trials. Thus, each child has two composite proprioception error scores, one for time 1 and one for time 2. We conducted a MANOVA analysis to investigate whether the intervention had a significant impact on manual dexterity, balance, throwing, enjoyment of physical activity, and proprioception. We analysed significant interactions using Bonferroni-corrected post hoc tests.

Two participants in the French group did not provide a date of birth. They were assumed to be 5 years-old for the purposes of calculating standardised scores for balance, manual dexterity and throwing. Calculating BPVS scores requires a more specific age in months and years. Since we did not have date of birth for these two individuals, we did not calculate BPVS scores for them. Two children were excluded from the MANOVA analysis: one child in the dance group (ASD diagnosis) was not able to complete the BPVS or proprioceptive tasks, and one child in the PE group failed both attempts of the manual dexterity task at time 1.

We conducted a compromise power analysis using G*Power 3.1 software (Faul et al., 2007). We entered the following parameters: effect size f=0.3, beta/alpha ratio=0.5, total sample size=48, number of groups=3 (dance, PE, French), and number of measurements=2 (time 1, time 2). Given these parameters, we had power of 0.82 to detect interactions with our MANOVA analysis.

5.3 Results

None of our hypotheses was supported. We did not find an interaction between group and time on proprioception $F(2, 43)=0.441$, $p=.647$, $\eta p^2=0.02$. We did not find an interaction between group and time on general movement skills: manual dexterity $F(2, 43)=2.101$, $p=.135$, $\eta p^2=0.089$, throwing $F(2, 43)=0.363$, $p=.698$, $\eta p^2=0.017$, or balance $F(2, 43)=0.238$, $p=.789$, $\eta p^2=0.011$. We did not find an interaction between group and time on enjoyment of being active $F(2, 43)=0.274$, $p=0.762$, $\eta p^2=0.013$. Enjoyment of being active (scores out of five) was high across all groups: French ($M=4.71$, $SE=0.15$; dance $M=4.59$, $SE=0.19$; PE $M=4.44$, $SE=0.15$).

5.3.1 Additional Findings

We found additional main effects of time. Proprioceptive error was significantly lower (better proprioception) at time 2 ($M=13.25°$, $SE= 0.39°$) than at time 1 ($M=14.95°$, $SE=0.52°$) $F(1, 43)=8.219$, $p=.006$, $\eta p^2=0.16$ (Figure 5. 2a). Manual dexterity scores were significantly higher at time 2 ($M= 8.35$, $SE= 0.59$) than at time 1 ($M=6.72$, $SE=0.58$) $F(1, 43)=5.765$, $p=.021$, $\eta p^2=0.118$ (Figure 5. 2d).

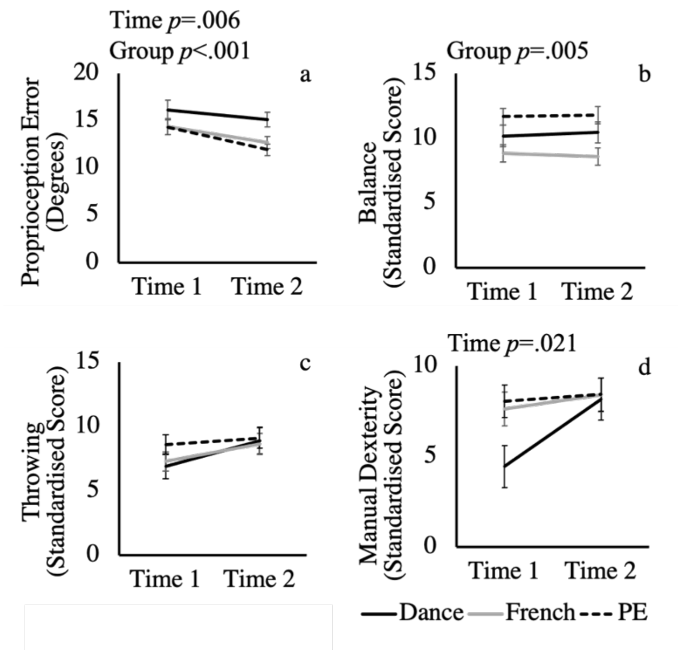

Figure 5. 2. Movement skill performance for all intervention groups at time 1 (pre-intervention) and time 2 (post-intervention). Proprioception Error (degrees), lower scores indicate better proprioception (a). Balance, higher scores indicate better performance (b). Throwing, higher scores indicate better performance (c). Manual Dexterity, higher scores indicate better performance (d). Error bars show standard errors. Significant main effects (with *p* values) are listed above each sub-plot where relevant.

We also found additional main effects of group. There was a significant effect of group on proprioception $F(2, 43)=4.08$, $p<.001$, $\eta p^2=0.974$ (Figure 5. *2*a). Error was significantly higher in the dance group (M=15.62° SE=0.70°) than the French group (M=13.16°, SE=0.55°) p=.028. There were no other significant group differences for proprioception. Proprioceptive error in the PE group was M= 13.52°, SE = 0.55°. There was a significant effect of group on balance $F(2, 43)=6.05$, $p=.005$, $\eta p^2=0.22$ (Figure 5. *2*b). Balance in the French group (M=8.71, SE= 0.62) was significantly poorer than in the PE group (M=11.72, SE=0.60) p=.004. There were no other significant group differences for balance. Balance in the dance group was M=10.32, SE=0.77.

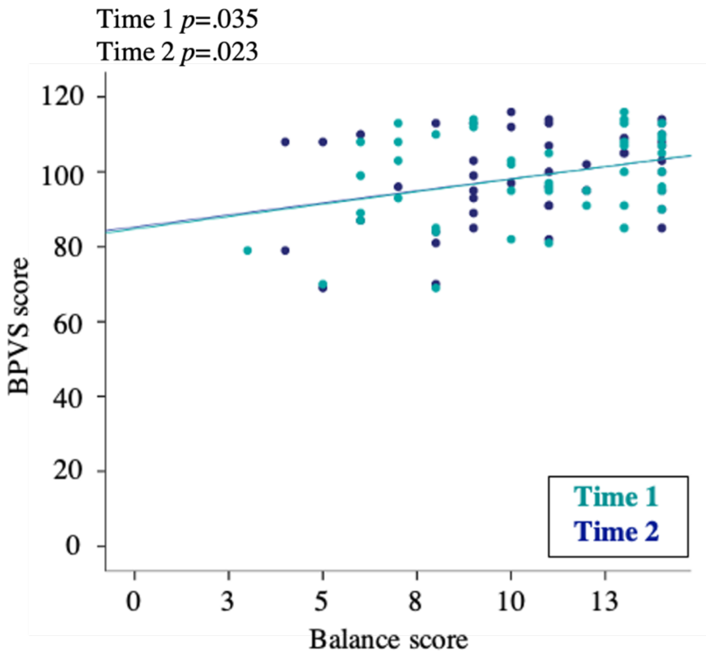

Figure 5. 3. Standardised balance scores and BPVS scores. All BPVS scores were recorded at time 1 only. Balance scores were recorded at time 1 (teal dots) and time 2 (blue dots). Significant correlations (with p values) are listed at the top of the figure.

Since we found significant effects of group on balance and proprioception, we wanted to assess whether this might be related to group differences in BPVS score using Pearson correlations. There was no correlation between proprioception and BPVS score at time 1 r=-.15, p=.324, or time 2 r=-.03, p=.837. However, balance did correlate significantly with BPVS score at both time 1 r=.316, p=.035, and time 2 r=.337, p=.023 (Figure 5. 3).

5.4 Discussion

We provided 5- to 6-year-olds with weekly activity sessions (dance, PE, French) in school for six weeks. Following these six weeks, all children improved on measures of whole-body proprioception and manual dexterity. In contrast, gross motor skills (balance and throwing) remained stable over time. Contrary to our predictions, physical activity sessions did not have significant positive effects on children's proprioception or general movement skills, even when the physical activity was specifically designed to improve proprioception. There were also group differences in performance for balance and proprioception, both before and after the activity sessions. Despite this, children in all groups rated physical activity as very enjoyable both before and after the activity sessions.

5.4.1 Weekly Sessions Are Not Enough

We predicted that general movement skills (manual dexterity, throwing and balance) would improve in the dance and PE groups to a greater extent than in the French group. We also expected that proprioception would improve to a greater extent in the dance group than in the PE or French groups. Dance was a strong candidate for a targeted, varied motor intervention with proven benefit for proprioception among both professional dancers (Jola et al, 2011; Kiefer et al., 2013) and children (Chatzopoulos, 2019; Chatzopoulos et al., 2018). We also felt that creative dance would be particularly effective since varied motor practice is important for successful motor learning (Adolph et al., 2018; Lee et al., 2017; Ossmy et al., 2018). However, we did not find any specific significant impact of dance training on children's general movement skills or proprioception. This is despite the dance sessions being specifically designed to train proprioception in varied and engaging ways.

Our findings contrast with previous work by Chatzopoulos and colleagues who found significant positive effects of dance intervention on children's proprioception. However, in Chatzopoulos et al's studies, dance training was delivered twice weekly over eight weeks (Chatzopoulos et al., 2018) or three months (Chatzopoulos, 2019), compared to just six weeks in the present study. Secondly, Chatzopoulos et al's studies excluded children with musculoskeletal injury, previous dance or sport training, and those with learning disabilities. In the present study, we adopted an inclusive approach and did not specifically exclude any child on the basis of injury, disability, dance/sport experience, or learning difficulty. Therefore, our sample was likely more diverse and representative of a typical UK classroom than that of Chatzopoulos (2019) and Chatzopoulos et al (2018). Thirdly, Chatzopoulos (2019) used classical ballet training, which is fundamentally different from the approach used in the present study. Although Chatzopoulos et al (2018) also used creative dance, the activities and techniques used were likely different to those in the present study. Finally, Chatzopoulos et al used a simple, single limb proprioception task. We measured whole-body proprioception since we felt this was more reflective of everyday movement demands. To train a complex, multi-limb sensorimotor skill, a longer period of training, or more regular training may be required.

Longer-term more regular dance training may have resulted in significant improvements in proprioception above and beyond those experienced in the control groups. However, it is also possible that the proprioceptive task itself explains why we did not find significant benefits of dance for proprioceptive memory. Firstly, the whole-body task was very complex. Indeed this was our intention – to measure children's ability to coordinate all four limbs into novel positions. However, perhaps dance training would have improved proprioceptive memory performance for a slightly simpler task (such as remembering a two-limb position). Secondly, the task required children to *remember and reproduce* complex whole-body positions. Again, this was our intention – in order to learn new motor skills, children must indeed be able to remember particular body positions and remember and reproduce them next time they attempt that particular skill. However, this memory element may have been too cognitively challenging for young children. It is possible that the dance training may have improved complex whole-body proprioception if this were tested 'online' - without the memory component. Thirdly, the task was completed in a lying down position which is not necessarily reflective of the training children received. During dance sessions, children were moving, balancing, creating dynamic positions in a variety of postures (standing, sitting, lying). It is possible that there was a disconnect between the task and the training. Nonetheless, it remains ecologically useful to test whether an engaging, creative dance training program (as might reasonably be delivered in school) would have broader, transferable effects on complex proprioceptive memory.

5.4.2 Stability and Improvement of Movement Skills at Five to Six Years

In all groups, proprioception improved significantly over time. This contrasts with our prediction that proprioception would improve to a greater extent among the dance group than the French or PE group. Although the dance intervention did not have a significant effect on proprioception, we have shown that complex, whole-body proprioception is developing rapidly at 5- to 6-years. This builds upon other previous literature showing rapid development in proprioception at this age (Contreras-Vidal, 2006; von Hoftsen & Rösblad, 1988). That said, we acknowledge that a plausible alternative explanation of our results is that children may simply have been more familiar with the proprioception task at time 2.

We also predicted that general movement skills (manual dexterity, throwing and balance) would improve to a greater extent in the dance and PE groups compared to the French group. However, we found that throwing and balance remained stable over time in all groups, whilst manual dexterity improved in all groups. Our finding that manual dexterity improved over a period of less than 2 months emphasises how rapidly children's fine motor skills are improving at this age. This compliments previous work showing improvements in manual control between 4- to 5-years and 6- to 7-years (Flatters, Hill, Williams, Barber, & Mon-Williams, 2014). It is interesting that manual dexterity and balance did not show similar patterns of change, since these two variables have been found to correlate (albeit modestly) in children aged 3- to 11-years (Flatters, Mushtaq, et al., 2014).

Our finding that children's fine motor skills (manual dexterity) improved, whilst gross motor skills (balance and throwing) did not could be partly attributed to the wider sociocultural context (and associated physical context) which shapes the motor experience of children (Adolph & Hoch, 2019). In particular, the typical western/industrialised school environment emphasises fine motor activities more so than gross motor. In western/industrial societies, children typically have extensive opportunity to develop fine motor skills through large amounts of time spent engaged in pen-paper classroom activities. In one Australian study, researchers observed primary school classroom activities over 5 days and found that at just 5- to 6-years old, children spent 62 minutes per day engaged in hand writing (McMaster & Roberts, 2016).

Previous work finds that balance is also undergoing important developmental change at 4- to 6-years (Shumway-Cook & Woollacott, 1985). However, we found no changes in children's balance. We also found no change in children's throwing performance. This contrasts with other findings. For example, in a study of US 2- to 6-year-olds, throwing to a target performance improved over an eight week period even in those who did not practice (Hicks, 1930). In a more recent study, Finnish 4- to 5-year-old's throwing skills improved significantly over twelve months, even without intervention (Livonen, Saakslahti, & Nissinen, 2011). These studies showing improvement in throwing measured performance over a longer time period than the present study. It seems likely that our short study was not long enough to detect developmental change in these skills. Nonetheless, our mixed pattern of change (improving manual dexterity and proprioception) and stability (stable throwing and balance) in children's movement skills highlights that not all sensorimotor skills have the same developmental profile (Kamm et al, 1990). To fully understand the asynchronous nature of sensorimotor development, a variety of different measures is required.

5.4.3 Movement Skills Vary Significantly Among Five to Six Year-Olds

We did not predict main effects of group on movement skill. However, there were significant differences in both balance and proprioception across groups at both time points. Specifically, balance was significantly worse in the French group than the PE group, and proprioception was significantly worse in the dance group compared to the PE group. These results highlight the disparity in motor ability between different groups of UK children. This suggests that not all children receive the same level of support, or the same opportunity to develop their motor skills.

Like balance and proprioception, the children's BPVS scores were also significantly different across groups. The French group performed significantly more poorly than the PE group. Our analyses show that BPVS scores at time 1, correlated significantly with balance at both time points. Previous work also suggests that there may be a link between language development and gross motor development. For example, in infancy, walking onset is associated with increasing receptive and productive language when controlling for age (Walle & Campos, 2014). However, since we were not specifically predicting or measuring relationships between language and motor skill, such post-hoc explanations are speculative. Other variables which we did not measure might be influencing both balance and vocabulary scores, without balance and vocabulary necessarily influencing each other.

As mentioned previously, the sociocultural context in which children grow up can impact their development (Adolph & Hoch, 2019). Socioeconomic status (SES) could also be an influential factor in the observed group differences in balance and vocabulary. Looking at the Index of Multiple Deprivation for each school's post code reveals that the French and dance groups were located in areas with a notably higher Deprivation Index rank than the PE group. A previous study by McPhillips and Jordan-Black (2007) found that children from higher SES areas score more highly on both motor development and receptive vocabulary than children from lower SES areas, using the same measures as the present study (MABC and BPVS). It is possible that SES could contribute to our observed group differences in both sensorimotor and language abilities. The difficulty in equating groups on all demographic measures is a key limitation of non-randomised control designs. Because the activity sessions were delivered in school, it was not possible to randomly assign participants to groups. Consequently, the children in each group may differ from the other groups in significant ways, such as socioeconomic status, despite all schools being in the same geographic region.

5.4.4 Five to Six Year-Olds Enjoy Being Physically Active

We predicted that PE and dance would improve enjoyment of physical activity. However, we found that 5- to 6-year-olds in all groups rated physical activity as highly enjoyable, both before and after the activity sessions. We acknowledge that children may be biased to respond at the extreme end of a likert scale. Nonetheless, we show that children rate physical activity extremely positive, and not extremely negative. This is a very encouraging finding. We should promote and maintain this enjoyment of physical activity to mitigate declining physical activity as children get older. From just 7 years children's physical activity levels begin declining (Farooq et al., 2018). Enjoyment of physical education predicts physical activity levels in both childhood (Sallis et al., 1999) and adolescence (Woods, Tannehill, & Walsh, 2012). Therefore, maintaining enjoyment of physical activity could help maintain physical activity levels as children get older.

5.5 Conclusions

Six weeks of physical activity sessions did not have a significant impact on children's proprioception or general movement skills. This was even true for a dance intervention, which was specifically designed to improve children’s proprioception on a whole-body task. We conclude that longer term, more intensive activities are needed to produce meaningful change in a complex sensorimotor skill. Gross motor skills (balance and throwing) remained stable over time, suggesting that children need greater support or opportunity to develop these skills. We also found significant group differences between children for balance and proprioception. Again, this suggests that the support and opportunity for children to develop movement skills is unequal. Despite this, we found that 5- to 6-year-olds rate physical activity as very enjoyable and showed improving manual dexterity and proprioception over time in all groups.

Chapter 6

General Discussion

6.1 Thesis Aims

The aim of this thesis was to describe sensorimotor development from a whole-body perspective. We aimed to determine the cues that children use to plan and control their movement and to investigate how children's sensorimotor abilities change with age and experience. We addressed these aims through the two main areas: visual control and proprioceptive control of action.

We have made a number of novel contributions to the literature. Firstly, we have mapped the developmental profile of visually guided stepping in mid-childhood for the first time. In doing so, we demonstrate that at just 6 years, children show adultlike reliance on vision to control precise stepping movements. Secondly, we have shown children's impressive motor planning skills by observing them in tasks reflective of everyday behaviours. In a research first, we manipulated how far ahead children could see whilst walking in a complex environment. We found that, like adults, children place their feet with caution when they cannot plan at least 2 steps ahead. Thirdly, by adopting a whole-body approach, we identified a number of asynchronies in sensorimotor development, including asynchronous development of arm and leg movements, as well as asynchronous development of visual and proprioceptive control. In particular, we show that whilst children develop sophisticated visual control strategies early in development, proprioception is much slower to mature.

In this discussion, we will outline the key findings of this thesis and its contribution to the sensorimotor literature more broadly. We will then discuss the practical implications of this work, its relationship with work on developmental coordination disorder, its limitations, and potential future directions for research in this area before summarising our conclusions.

6.2 Summary of Key Findings

In this section we summarise the key findings of this thesis for visual control and proprioceptive control.

6.2.1 Part 1 – Visual Control

From the existing literature, it was not clear whether children can use continuous visual feedback to fine-tune precise stepping movements like adults. Therefore, in study 1 we measured children's precision stepping performance, whilst manipulating the availability of visual feedback. The key research questions of study 1 were: do children use continuous visual feedback to guide precise stepping movements? And, does visually guided action develop in a limb-specific, or limb general manner? To answer these questions we compared stepping and reaching performance with and without continuous visual input. We found that children aged 6- to 8-years use online visual feedback to fine-tune both stepping and reaching movements. Even at just 6 years, children relied on vision to control precision stepping to the same the extent as adults. For both stepping and reaching, children's error increased when vision was occluded at movement onset. Despite both being visually guided, reaching and stepping had very different developmental profiles. To our knowledge, this is the first study to examine the development of visually guided precision stepping and the first study to compare stepping and reaching.

Having established that even young children use online vision to control precision stepping, we turned our attention to the more complex, whole-body skill of walking. Previous work has not clearly documented how children control walking on long or complex paths, especially when the feet must be placed into very specific locations. Therefore, in study 2, we measured children's foot placement and speed as they walked over a series of targets, whilst manipulating how many of the upcoming targets could be seen (1, 2, or 3 steps ahead). The key research question of study 2 was: how do children use vision to control complex walking – do they plan ahead or guide each step one at a time? We found that like adults, children use distal visual cues to plan their walking. When vision of the upcoming terrain was restricted, children and adults behaved with caution, reducing walking speed and foot placement error. Further, both children and adults placed their feet more carefully during conditions of postural threat. Children achieved these sophisticated adjustments despite their foot placement during walking being overall less accurate and more variable than adults'. This is the first study (to our knowledge) to directly manipulate the availability of upcoming visual information as children walk in a complex environment.

6.2.2 Part 2 - Proprioceptive Control

The developmental literature had not directly tested whether children benefit from forward models for proprioception. To address this gap, in study 3 we assessed children's ability to remember and reproduce target arm and leg movements, whilst manipulating whether the target movement was performed actively (forward model generated) or passively (no forward model generated). The key research question of study 3 was: do children benefit from forward models for memory-based proprioceptive judgements? Children's proprioceptive judgements were poorer than adults' and were similar following active and passive target movements. Therefore, we did not find evidence of children benefitting from forward models for memory-based proprioceptive judgements. To our knowledge, this is the first study to directly manipulate the availability of forward models during a proprioceptive judgement task in children and the first study to test proprioception of both the arms and legs in children.

Having established that children find even simple, single limb proprioceptive judgements challenging, in study 4 we sought to improve children's proprioception through physical activity. We focused on improving complex, whole-body proprioception, since natural movement involves the coordination of multiple limbs simultaneously. The key research question of study 4 was: can children's whole-body proprioception be improved through dance? We asked children to remember and reproduce whole-body positions and measured their performance before and after a six-week creative dance program. We also included two control groups: one received six weeks of standard, non-creative physical activity sessions and the other received six weeks of French classes (no movement). We found that six weeks of creative dance training were not enough to significantly improve children's proprioception. This is despite the dance sessions being designed to target proprioception. Nonetheless, children's proprioception in all groups improved over the course of the study, as did their manual dexterity performance. In contrast, balance and throwing skill remained stable. No previous study (to our knowledge) has attempted to train and measure complex, whole-body proprioception in children.

6.3 Contributions to the Literature

In this section, we discuss the contribution of this thesis to the literature on sensorimotor development.

6.3.1 Sensorimotor Development Continues Throughout Childhood

Sensorimotor development is a long and slow process – we demonstrated this for both stepping and walking as well as for proprioceptive judgement tasks. In study 1, we showed that precise stepping movements continue improving throughout mid-childhood. In study 2, we studied foot placement in the more complex, whole-body task of walking. Here, we found that even at 8 years children cannot place their feet as accurately as adults. Similarly, Corporaal et al (2018) found that variable error for foot placement during walking continues to decrease even into adolescence, suggesting ongoing development even up to 18 years. Walking begins in infancy and at just 3 years children show very sophisticated walking in complex, multiple-obstacle environments (Mowbray & Cowie, 2020). Nonetheless, precise foot placement during walking when landing locations are tightly constrained matures much later. By measuring foot placement in detail using motion capture, we have shown that even though children can successfully walk in complex terrains without falling, the manner in which they place their feet is far from adultlike as late as 8 years and likely for many years to follow (Corporaal et al., 2018).

Proprioception also has a protracted developmental profile. In study 3, we found that proprioception was significantly poorer in children aged 4- to 13-years than adults, suggesting that proprioception is immature even in adolescents. This aligns with findings from Holst-Wolf et al (2016) who found proprioception continued improving even at 17 years. Finally, study 4 provided a rare opportunity to measure children's sensorimotor progress over a relatively short period. We found that not all sensorimotor skills show significant improvement over the course of one school term (e.g. throwing and balance did not improve). Together, these findings emphasise that sensorimotor development is a long and slow process, ongoing throughout childhood. Further, even when we introduced a creative dance program specifically designed to improve proprioception, this had no significant effect on proprioception after 6 weekly sessions. Children likely need at least bi-weekly sessions to improve proprioception through dance (Chatzopoulos, 2019; Chatzopoulos, Doganis, & Kollias, 2018). This further emphasises the large amount of time and experience that is required for sensorimotor development.

By evaluating children's sensorimotor skill relative to adults' there is an implication that sensorimotor skill reaches a fixed, mature adult state. However, this is simplistic and in fact untrue. Sensorimotor development occurs throughout childhood but also continues throughout the entire lifespan, taking different forms for different individuals. For example, the characteristics of adult walking vary between and within individuals, depending on many factors, including: cultural norms (Adolph et al., 2018), pregnancy (Forczek et al., 2019), weight status (Browning, 2012), cognitive load (Ellmers et al., 2016) and ageing mediated by fall-related anxiety (Ellmers et al., 2019). In summary, sensorimotor behaviour evolves throughout the lifespan. In this thesis we have focused on one small part of sensorimotor development in the primary school age range.

6.3.2 Mature Visual Strategies Before Mature Movement Execution

Even where children show poorer movement execution than adults (in terms of accuracy or precision), they nonetheless show sophisticated sensorimotor strategies. In study 1, children aged 6 years used visual feedback to control stepping movements to the same extent as adults, even though their performance was overall less accurate and more variable than adults'. In study 2, children adjusted walking behaviour depending on the availability of distal visual cues, despite their foot placement remaining immature. When they were unable to see at least 2 steps ahead, both children and adults placed their feet more carefully. These important new findings build on previous eye tracking research. Franchak and Adolph (2010) showed that children walking in complex environments visually fixate obstacles in advance but did not assess whether this visual behaviour influenced foot placement. We can now conclude that children do use visual cues to plan foot placement, even despite their foot placement error being high relative to adults'.

Our results show that in the domain of visual control, sophisticated visual guidance of action comes long before mature movement execution. Similarly, Mowbray and Cowie (2020) showed that despite overall more variable foot placement than adults, 3- to 5-year-olds do adjust foot placement to accommodate upcoming obstacle sequences, demonstrating similar visually guided planning during walking to adults. We can now add that beyond the preschool years, children tackle ever more complex tasks (such as walking over irregular targets) with adultlike planning skills, even as movement execution remains immature. Further, children can flexibly use different modes of control depending on the nature of the task: using online visual feedback to fine tune precise stepping movements and using feedforward visual planning during complex walking tasks.

In this thesis, we show that within the visual domain, children demonstrate a sophisticated ability to plan in complex environments and match their sensorimotor strategy to the demands of the task and the environment. Is children's sophisticated, flexible motor behaviour a demonstration of sophisticated and flexible cognition? As infants develop the physical capacity to take on ever more complex motor challenges (e.g. crawling, standing, walking), they must learn cognitive skills: how to gather, process and respond to rich environmental information through their senses (Adolph, 2008). Children master these complex (and arguably cognitive) skills before their basic movement execution is mature. Complex cognition and motor control may even develop from a common source: the need to control action (Gottwald et al., 2016). Indeed, prospective motor control in infancy correlates positively with infants' executive functioning (Gottwald et al., 2016). Similarly, early gross motor skills (measured during infancy and preschool years) are predictive of working memory and processing speed during the primary school years (Piek, Dawson, Smith, & Gasson, 2008). Later, at 9- to 18-years, foot placement accuracy during walking correlates with both lower grey matter volume (banks of the superior temporal sulcus) and maturation of white matter tracts (connecting higher level brain regions), perhaps suggesting a relationship between children's motor performance and higher level cognition (Corporaal et al., 2018). In summary, through movement children learn complex cognitive skills like using visual information to plan and select appropriate motor strategies for complex tasks and environments. Learning to flexibly select appropriate motor strategies takes precedence over developing mature movement execution.

6.3.3 Sensorimotor Skills Develop Asynchronously

Sensorimotor skills develop asynchronously. Asynchronous development of the sub-systems required for movement lead to non-linear development (Kamm et al., 1990). For example, infants make frequent stepping movements early on, but stepping behaviour is later inhibited by a lack of strength relative to the weight of the legs (Kamm et al., 1990; Thelen, Fisher, & Ridley-Johnson, 1984). Different components of movement (e.g. strength, cognition, balance, sensory perception, motivation) develop at different rates, meaning that motor skills (e.g. fine vs. gross motor, arm vs. leg movement, visual vs. proprioceptive control) also develop at different rates. By taking a whole-body perspective and by using complex whole-body tasks, in this thesis we have shown that asynchronies also manifest in a number of ways in older children. We have identified developmental asynchronies that had not previously been documented.

Firstly, sensorimotor development is limb-specific. In study 1, we showed that visually guided reaching and stepping develop asynchronously and in study 3, we showed that proprioceptive judgements for the arms follow different patterns to those with the legs. This is despite both stepping and reaching both being visually guided and having similar kinematic profiles in adulthood (Jakobson & Goodale, 1991; Reynolds & Day, 2005). Secondly, fine and gross motor skills have different developmental profiles. In study 4, we showed that gross motor skills (balance, throwing) develop differently to fine motor skills (manual dexterity). This supports the norm of treating fine and gross motor skills separately in standardised movement assessments (Cools et al., 2009). Finally, good performance on a simple, single limb task does not necessitate equally proficient performance on a related complex, whole-body task. In study 1, children's performance on a single step task was not significantly different to adults' at 8 years. However, during walking children's foot placement error was significantly higher than adults' in study 2. Precision stepping ability did not transfer from a simple single step task to a more complex walking task. This aligns with the work of Adolph and colleagues who have shown that motor learning does not translate across different but closely related tasks. For example, newly crawling infants make safe decisions about reaching over a large drop from a sitting posture, but then fall straight into the same gap when reaching from a crawling posture (Adolph, 2000). Performance on even very closely related sensorimotor tasks is asynchronous.

There are also asynchronies between sensory modalities. In the context of this thesis, visual and proprioceptive control develop differently. Earlier work by von Hoftsen and Rösblad (1988) found that 5- to 12-year-olds were significantly better at pointing to targets specified visually than to targets specified proprioceptively. Similarly, in this thesis we also clearly show that children develop relatively skilful visual control mechanisms early in development. In contrast, we found no evidence of adultlike feedforward mechanisms on a memory-based proprioceptive task across the whole childhood age range (up to 13 years). Our findings suggest that visual control matures before proprioceptive control. This has consequences not only for proprioceptive functioning but also for multisensory performance. Nardini et al (2013) showed successful multisensory integration (i.e. better target localisation when given both visual and proprioceptive cues) among children for whom proprioceptive target localisation was less than twice as variable as visual target localisation. In other words, children must first develop good proprioception before they can effectively integrate proprioceptive information with visual information. Why might proprioceptive control take longer to develop? Physical growth continues throughout late childhood, and adolescence marks a particularly significant time of physical change (Quatman-Yates et al, 2012). The rapid changes in dimensions and dynamics of the body during childhood and adolescence likely make developing an accurate sense of limb position very challenging.

Thus proprioception is likely more heavily impacted by physical growth than is visually guided control, since vision is mature in adolescence.

6.3.4 *Applying Theories from the Adult Literature to Children*

In study 2, we used the critical control phase hypothesis (Matthis et al., 2017) to make predictions about children's visually guided walking. Based on the work of Matthis and colleagues, we expected that children would use visual cues from 2 steps ahead to control their walking like adults do. The critical control phase hypothesis is a particularly good theory to apply in developmental work because it is body-scaled: it predicts visual sampling from 2 steps ahead, as opposed to visual sampling from a specific distance ahead or a specific amount of time in advance. This means that the same prediction can reasonably be applied to both children and adults, despite children having shorter legs and smaller steps. Indeed, we found that the 2 steps ahead visual window was also important in children's visually guided walking. By using theory from the adult literature, we were able to test detailed predictions about complex sensorimotor control in children.

In study 3, we tested the theory that forward models generated during active movement have benefits for the performance of memory-based proprioceptive tasks. We found no evidence that children benefitted from forward models, although adults did. However, it remains unclear whether i) children do not generate forward models for active movement, or ii) children generate forward models but do not benefit from them for memory-based proprioceptive judgments. Previous papers have drawn strong conclusions about such null results. Capaday et al (2013) and Darling et al (2018) used a proprioceptive task in which blindfolded participants attempted to oppose their index fingers (their target arm was positioned actively or passively). In both studies, there was no difference in performance in the active condition compared to passive. Since there was no evidence of better performance in the active condition, the authors concluded that we do not need to invoke the concept of forward models (Capaday et al., 2013) and even that the results cast doubt on the existence of forward models (Darling, et al., 2018). Based on this reasoning, the findings of study 3 show that children do not generate forward models for memory-based proprioceptive tasks. If this is the case (that children do not generate forward models), then the theory is somewhat of a red herring for developmental research on proprioception. However, (as discussed later in 'Future Directions and Limitations') further research using neuroimaging may be able to clarify this issue.

6.4 Practical Implications

Sensorimotor development is ongoing throughout childhood and into adolescence. The implication of this is that children need opportunity and support to practice their sensorimotor skills throughout the primary school age range and beyond. There is no critical cut-off period after which development is ‘complete’. Children also need the opportunity and support to practice a variety of whole-body movements. Arm and leg movements, visual and proprioceptive control mechanisms, and fine and gross motor skills all develop asynchronously. Therefore, experience in one type of skill (e.g. fine motor, or manual skills) does not necessarily translate into improvements in other skills (e.g. gross motor, or lower limb skills). Further, children need the opportunity to practice their whole-body movement skills regularly. In study 4, we showed that even a targeted proprioceptive intervention was not enough to improve proprioception when delivered once a week for 6 weeks. Notably in study 4, we also found that proprioception and balance skills were significantly different across groups of children within the same geographic region. This inequality in sensorimotor skill may have implications for the performance of everyday behaviours (like getting dressed, or walking across a cluttered room), as well as for physical fitness (Utesch, Bardid, Busch, & Strauss, 2019), mediated by a relationship between motor competence and engagement in physical activity (Stodden et al., 2008). To ensure that all children develop the necessary sensorimotor skills, children of all ages need varied, regular, whole-body movement experience.

6.5 Developmental Coordination Disorder

Further practical implications become apparent when we consider the present research alongside similar research that has been conducted with children with developmental coordination disorder (DCD). Individuals with DCD experience a range of deficits in the sensorimotor domain, for example: forward modelling, rhythmic coordination, executive function, gait and postural control, catching and interceptive action, and sensory perception (Wilson, Ruddock, Smits-Engelsman, Polatajko, & Blank, 2013). In the following paragraphs we discuss: 1) the importance of physical activity engagement for all children, regardless of sensorimotor ability; 2) that the development of complex movement planning and adaptation takes precedence over movement execution per se; and 3) the implications of our findings on forward models for explaining proprioceptive deficits in DCD.

Varied, regular, whole-body movement is indeed crucial for motor development. However, engagement in physical activity and enjoyment of being active may be just as important as the development of sophisticated sensorimotor skills per se. The literature on DCD provides insight into how we might approach movement skill and physical activity engagement for children more generally. Green et al (2011) found that boys with DCD (tested at 7- to 8 -years) have significantly lower physical activity levels at 12- to 13-years than their peers with typical motor development, whilst girls had low levels of physical activity levels regardless of motor skill status (Green et al., 2011). Among boys, poor targeting skills (throwing a beanbag to target) was significantly associated with reduced physical activity levels (Green et al., 2011). The authors argue that children with DCD need opportunities to engage in varied forms of physical activity, especially those that do not involve targeting skill, to promote enjoyment of physical activity. Similarly, Cairney et al (2005) found that 9- to 14-year-olds with DCD perceived themselves as having poorer physical skills and lower enjoyment of physical education than peers with typical motor development. Further, 28% of the variance in children's physical activity levels was predicted by DCD and physical activity self-efficacy. Again, these authors argue that it is important to find activities which children can enjoy and be successful at, despite their motor difficulties. A different approach would be to try to directly improve the movement skills of children with DCD – this is similar to the approach we took in study 4 with children who did not have reported DCD diagnoses.

In study 4, we used creative dance to try to improve children's sensorimotor skills. However, we did not find a significant impact of 6 weekly sessions on children's sensorimotor skills. Here we might learn from the message of DCD researchers e.g. Cairney et al (2005) and Green et al (2011). Improving children's movement skills through intervention is a desirable goal. However, perhaps an equally important (and possibly more immediately achievable) goal is facilitating enjoyable engagement in physical activity for all children to promote both physical and mental wellbeing. By using creative dance, we were able to engage a whole class of children in physical activity every week. In creative dance there is no right or wrong and no specific techniques to master. Whilst organised games and competitive sport have their place in physical education, free-form movement like dance can be a powerful tool for ensuring that all children of all abilities can engage in movement in an enjoyable way.

Similarly, developing mature movement execution skills per se is important but it does not supersede the importance of learning to move adaptively in complex environments. Together, the literature on DCD and our research with young typically developing children show that adultlike accuracy and precision in movement execution are not pre-requisites for sophisticated motor planning and adaptation. In part 1 of this thesis, we found that 8-year-olds use distal visual cues to plan ahead like adults when walking in complex environments - even though their foot placement error during walking was high and their balance relatively poor compared to adults. Similarly, other researchers have investigated walking in complex environments in children with DCD. Compared to walking on an even surface, when walking on an irregular surface individuals with DCD make more marked adaptations to walking then their typically developing peers – they use slower, wider steps and walk with their head angled downward to a greater extent (Gentle, Barnett, & Wilmut, 2016). These adaptations are cautious behaviours, facilitating safer walking in a complex terrain. More recently, researchers have found that although 8- to 15-year-olds with DCD show higher foot placement error during walking, they display similar gaze behaviour and anxiety levels as their typical peers (Parr, Foster, Wood, & Hollands, 2020). Further, both typical children and those with DCD made more distal fixations when there were obstacles present in the upcoming walkway (Parr et al., 2020). Therefore, like their typical peers, children with DCD use visual cues to plan ahead during walking. Together this research suggests that children with

DCD engage in complex planning and adaptation when walking in complex terrain, despite their gait being atypical. This is similar to what we observed in typical children: although foot placement error during walking was high at 8 years, children still engaged in sophisticated planning and adaptation to environmental conditions. In summary, 'typical' gait and 'mature' foot placement error are not prerequisites for sophisticated, adaptive motor behaviour in complex environments. In practical terms, we should not view atypical or immature motor execution as a barrier to adaptive behaviour in complex environments; nor as a barrier to physical activity engagement.

The present research also has implications for our understanding of a proposed mechanism of DCD. In study 3, we found no evidence that children benefit from forward models for memory-based proprioceptive judgements and children's proprioception was immature throughout childhood. This is particularly interesting since a deficit in forward model generation (leading to a reliance on slow sensory feedback for motor control) has been proposed as an explanation of DCD (Wilson, Thomas, & Maruff, 2002; Wilson et al 2016). This theory assumes that children with typical motor development successfully use forward models to control movement. However, the results presented in this thesis suggest that children do not benefit from forward models – at least not for memory-based proprioceptive tasks. Children with DCD do show deficits on proprioceptive tasks. For example, children with DCD are poorer than their typically developing peers at matching the position of their arm with the contralateral arm whilst blindfolded, and at using their unseen arm to locate a visual or proprioceptive target (Smyth & Mason, 2008). However, based on the results of study 3 (no evidence of typical children benefitting from forward models for a proprioceptive judgement task), we would not support a forward model deficit explanation of poor proprioception among children with DCD. Further research should directly manipulate the availability of forward models during proprioceptive tasks in both children with DCD and age-matched controls to further test the forward model deficit theory.

6.6 Future Directions and Limitations

In this section we discuss future directions for research to build on our findings and to address some key limitations of this thesis.

6.6.1 Longitudinal Designs

In study 1, we mapped the developmental profile of stepping and reaching between 6 and 8 years at the group level, using a cross sectional design. Similarly, in study 3 we also used a cross sectional design to look for changes in proprioception between 4 and 13 years. However, without measuring sensorimotor skills longitudinally (i.e. tracking the development of individuals over time), this thesis cannot describe the process by which stepping performance improved, or what the developmental trajectory of proprioception looks like for an individual child. To understand the process of change itself (as opposed to taking snapshots of an ability at timepoints years apart) we need to sample longitudinally and frequently (Adolph, Robinson, Young, & Gill-Alvarez, 2008).

Future work using longitudinal designs would be particularly useful for understanding variability in developmental trajectories. Throughout development, there are both increases and decreases in variability. As we become more skilled in a particular movement or task, performance becomes more consistent (Vereijken, 2010). In contrast, with greater skill and experience comes greater functional variability in terms of the ability to adapt to perturbations and environmental changes (Vereijken, 2010). Further, periods of increased variability in development can signal an imminent developmental change (Vereijken, 2010) – for example, a transition from uni-sensory to multisensory control of reaching (Hay, 1979). We also need to recognise that there can be huge variability in developmental trajectory between individuals. For example, the age of walking onset varies between infants depending on their walking experience and child rearing practices (Adolph et al., 2018). Future longitudinal studies can explore the variety of developmental pathways and sensorimotor strategies that children use beyond infancy.

Longitudinal studies would also be useful for studying development beyond childhood. In study 3, we found that proprioception was poorer among 4- to 13-year olds than adults, with no significant change across childhood. This suggests that proprioception is not mature even in adolescence. Adolescence is often thought of as a time of motor awkwardness, with many sensorimotor skills not fully mature by adolescence, including: visual control of posture, vestibular control and proprioception (Quatman-Yates et al., 2012). However, there are very few studies examining the developmental profile of sensorimotor skill throughout the adolescent period (Quatman-Yates et al., 2012). Future longitudinal studies should map sensorimotor development beyond childhood and through adolescence.

6.6.2 Training Studies

In studies 1 and 3, we mapped the development of sensorimotor skills cross-sectionally and compared children's performance to that of adults. However, we did not explore the extent to which sensorimotor development was driven by experience. Is children's sensorimotor performance poorer than adults' because children lack sufficient experience of sensorimotor control? Or do children lack physical/cognitive/neural maturity, such that even with training they cannot perform sensorimotor tasks like adults? Rather than pitting experience and maturation against each other, the question is better posed: to what extent does experience impact on sensorimotor performance in childhood? Key figures in developmental research would argue that experience has a huge impact on sensorimotor development. For example, Karen Adolph has written extensively on the impact of natural movement exploration and cultural differences on the development of walking (Adolph & Hoch, 2019; Adolph et al., 2018). To build on this, researchers need to empirically measure whether specific experiences (e.g.

training programmes) can significantly impact on specific aspects of sensorimotor development. Training studies can help us understand whether experience has a significant impact and what kind of experience is needed to have a significant impact. Moreover, training studies could help us to improve children's sensorimotor outcomes.

In study 1, we found that children's foot placement was less accurate than adults' for single stepping movements until 8 years. In study 2, we found that even at 8 years children's foot placement during walking was significantly higher than that of adults. Could there be ways to directly improve children's precision stepping ability? Previous studies have shown that gaze direction has a direct impact on foot placement (Chapman & Hollands, 2007; Smid & Den Otter, 2013). Instructing older adults to maintain gaze on a stepping target until after foot contact can significantly improve their foot placement during walking (Young & Hollands, 2010). Gaze training has also been used to improve throwing and catching performance in children with DCD. In a study by Wood et al (2017), two groups of children with DCD received group training for one hour per week, for 4 weeks. Both groups watched videos of an expert model completing a throwing and catching task. For the technical training (TT) group, the video focused on the models' movement. For the quiet eye training (QET), the videos focused on the model's gaze behaviour. After the training program, catching performance improved significantly more in the QET group than in the TT group. In summary, given their success in older adults and children with DCD, gaze training programs could potentially also improve typical children's sensorimotor performance.

In study 3, we found no evidence that children benefit from forward models for proprioceptive judgements. Therefore, we concluded that children rely predominantly on sensory feedback for proprioception. Since children do not benefit from forward models for memory-based proprioceptive judgments like adults, improving forward model use through training could promote improved proprioception in children. Work with children with DCD suggests that this type of training could be effective. In a study by Wilson et al (2002), a sample of 7- to 12-year-olds with low scores on the MABC (Movement Assessment Battery for Children) were divided into three groups: motor imagery training, traditional perceptual motor training, or wait-list control. The intervention groups received 5 weekly sessions, each lasting 60 minutes. The imagery training group engaged in: visual imagery exercises involving predictive timing, relaxation and mental preparation, visual modelling of fundamental motor skills, mental rehearsal of skills, and overt practice. The perceptual motor training group engaged in a combination of gross-motor (e.g. jumping, climbing, and marching) and fine-motor (e.g. hard writing, origami, and peg work) tasks. MABC scores improved significantly in both the intervention groups, suggesting that mental imagery training can improve motor performance in children with DCD by ameliorating a forward model deficit (Wilson et al., 2016, 2002). Future work should explore this approach with typical children who might also struggle to use forward models on sensorimotor tasks.

In study 4, we found that 6 weekly sessions of creative dance training did not significantly improve children's proprioception or general movement skills (manual dexterity, throwing, and balance). This is despite professional dancers having superior proprioception to non-dancers (Jola et al., 2011; Kiefer et al., 2013) and dance having significant positive effects on children's proprioception in previous studies (Chatzopoulos, 2019; Chatzopoulos et al., 2018). We conclude that to have a significant impact on sensorimotor skills, interventions need to be more regular or longer term. However, this must be balanced against the need for interventions that are low financial cost, low time investment, and easy to implement within the school day (Naylor et al., 2015). Future work should explore the potential for interventions designed to improve proprioception that can be implemented more regularly than once a week and over a longer period of time. An example model of a school-based physical activity intervention is 'The Daily Mile' in which children run, jog, or walk around 1 mile every day. Research has shown that, during just one academic year, children aged 4- to 12-years engaged in The Daily Mile programme showed significant improvement in activity levels, sedentary time, fitness, and body composition (Chesham et al., 2018). Future research should establish whether a similar approach could be used to train specific sensorimotor skills like proprioception through daily, targeted activities.

6.6.3 Multisensory Studies

In this thesis, we explored visual control and proprioceptive control in separate studies. However, typically both visual and proprioceptive cues are used to control our movements. Previous developmental work by Nardini et al (2013) found that children do not successfully integrate sensory cues from vision and proprioception until around 8 years – although some younger children with particularly good proprioceptive accuracy did show multisensory integration. This was demonstrated using a simple position matching task, in which children had to locate a target using: vision alone, proprioception alone, or both vision and proprioception together. For younger children, having multisensory information (vision and proprioception) does not generally improve their ability to locate targets (Nardini et al, 2013). However, fewer studies have taken a multisensory approach to study how children control ongoing movements. To what extent do vision and proprioception each contribute to the control of ongoing movements, like steps, reaches, or walking?

Future research could directly test the relative contribution of different sensory inputs by manipulating both visual and proprioceptive information during the same task. For example, Rapos and Cinelli (2020) studied the contribution of both vision and proprioception to walking over obstacles in children aged 9 years. They manipulated the number of obstacles in the path (visual information) and the walking surface (solid or foam). By manipulating the walking surface, the reliability of proprioceptive inputs is changed from high (solid surface) to low (foam surface). Such an approach allows researchers to measure the impact of both visual changes in the environment, and changes in the reliability of proprioception on children's walking control. This could be used to understand the extent to which children rely on proprioception for walking when the feet must be placed into tightly constrained target locations.

Another way to clarify the relative contribution of vision and proprioception to movement control would be to combine visual occlusion methods (as per study 1) with tendon vibration methods (to disrupt proprioception). Tendon vibration has been used in developmental studies of reaching. For example, Hay and Redon (1997) applied tendon vibration to children during arm movements and found that this systematically impacted movement direction. However, the same technique has not been used to study sensory control of stepping in children and future work should seek to combine both visual and proprioceptive manipulations. By manipulating both the availability of vision and proprioception during a stepping task, we could better understand the relative impact of each sensory system on stepping performance. As we have seen from the results of study 1, the developmental profiles of upper and lower limb control are not the same. Therefore, it is important that we explore both visual and proprioceptive mechanisms for the arms and legs separately.

6.6.4 Neural Bases

In part 1 of this thesis, we investigated the development of visually guided stepping and walking. We found that single step performance was improving between 6 and 8 years, and that during walking foot placement error remained high for 8-year-olds. We have already discussed that gaze behaviour, proprioception and multisensory integration might all contribute to development in lower limb sensorimotor control. However, development in all of these areas may be underpinned by neural changes. By studying the neural control of stepping and walking in development, we might begin to understand the mechanism by which visually guided walking improves in childhood. Corporaal et al (2018) measured foot placement error during walking and took MRI structural brain images from children aged 9- to 18-years. Both lower grey matter volume (banks of the superior temporal sulcus) and maturation of white matter tracts (connecting higher level brain regions) were associated with improvements in stepping accuracy. This supports the idea that neural maturation might be closely linked motor development and demonstrates a potential important link between higher level cognition and sensorimotor performance. However, the authors acknowledge that many other developmental changes (e.g. functional brain development, as well as changes in the musculoskeletal and central nervous systems) could also have an impact on stepping performance. In future, studies should consider multiple potential influences on stepping development and follow these changes longitudinally within individuals.

In study 3, we did not find any evidence that children benefit from forward models for performance of a memory-based proprioceptive task. However, our results do not tell us whether or not children actually generate forward models. It is possible that forward models were generated but were not beneficial for task performance. Future research could help to fill this knowledge gap by using neuroimaging to understand whether or not children generate forward models for active movements. If children do generate forward models, we might expect that patterns of brain activation would be different during active vs. passive movement. Some studies have addressed this hypothesis, but with contrasting results. Guzzetta et al (2007) used fMRI to compare activation in the contralateral primary sensorimotor cortex, ipsilateral cerebellum, supplementary motor area, and lateral pre- motor cortex during active and passive opening and closing of the hand in children and adults. In both adults and children, they found no significant difference in brain activation during active movement compared to passive. In contrast, in a sample of 11- to 17-year-olds Van de Winckel et al (2013) found that active movement elicited significantly greater activation than passive movement in a range of brain areas (primary sensorimotor cortex, pre-supplementary motor area, bilateral cingulate gyrus, right insula, right superior temporal gyrus, right lobules V, and area bordering lobules V–VI and the bilateral lobule VI). However, in this study active movement involved opening and closing of the hand, whilst passive movement involved the index finger only. Future research should seek to replicate the result of Van de Winckel et al (2013) but using comparable movements in the active and passive conditions.

6.6.5 Balance

In each of the studies presented in this thesis, efforts were made to measure or control for balance. This was because we know that balance plays a crucial role in the development of other motor skills. One of the greatest challenges for new walkers is to build the stability and strength to balance in an unstable bipedal stance – made even more challenging by the fact that an infant's head is large relative to its body (Adolph, 2002). Later, at 4- to 6-years, children show higher body sway than older children even when standing on a stable surface with full visual input available (Shumway-Cook & Woollacott, 1985).. When walking, children accommodate their instability by adopting a wider gait pattern to increase their base of support when moving through complex environments (Berard & Vallis, 2006; Gentle et al, 2016). Balance remains immature even in adolescence with 13- to 14-year-olds showing higher sway than adults when tested in a variety of visual and proprioceptive conditions (Barozzi et al, 2014; Blaszczyk & Fredyk, 2021; Golomer et al, 1999). We also know that balance has the potential to impact not just on stepping and walking, but also on even upper-limb fine motor control since a stable posture provides a stable base from which to control arm movements (Flatters et al, 2014). Despite all of this, in part 1 of this thesis, we did not find any significant relationships between our measures of balance and the performance of stepping, reaching, or walking tasks. We administered balance tests separately from the stepping, walking and reaching tasks. Therefore, the reason why we found no relationships between balance and stepping, walking, or reaching may simply be that our balance measures did not sufficiently approximate the balance demands of stepping, walking, or reaching.

Future studies should consider measuring balance during stepping, walking and reaching. This could be achieved by tracking the body's movement during the task using motion capture markers on the body, with greater sway indicating poorer stability. In simple single-step/reach paradigms, researchers could manipulate balance by having children step with and without a harness or handrail support (as per Reynolds & Day, 2005b with adults); or by asking children to reach to targets whilst sitting compared with standing. In walking tasks, asking children to walk on a foam surface can disrupt balance by rendering somatosensory cues unreliable. Comparing walking behaviour on a foam surface and a solid surface can help us understand the importance of balance for locomotor control (this approach was taken by Rapos & Cinelli, 2020). Embedding balance measures and manipulations into the main task may provide a more robust assessment of whether balance does indeed impact on stepping, walking, or reaching in children.

6.6.6 Virtual Reality

In study 2, we used VR to flexibly manipulate visual information as children and adults walked in a complex environment. The virtual set-up also allowed us to easily and safely manipulate postural threat without increasing the objective risk to participant safety. A further advantage of using VR was the ease with which we could scale the virtual environment to participant leg length – approximating task difficulty across children and adults and participants of different sizes. Nonetheless, there are some aspects of the VR environment which pose challenges for interpreting our findings. Most notably, that in VR, participants had no visual information about their body other than two coloured spheres representing their feet. This required participants to learn a new mapping between motor commands proprioceptive cues and the new visual representation of their feet. Given that young children find sensory remapping a challenge (Contreras-Vidal et al., 2005), this may have had a negative impact on children's performance of the task. Indeed we did find that foot placement error was significantly higher for 8 year-olds than adults in VR. It is possible, that in a non-VR version of this task (e.g. created with targets projected onto the floor) children would benefit from the usual mapping between motor commands, proprioception, and visual feedback from the legs, leading to lower foot placement error. As developmental research in this area progresses, it would be nice to see studies move towards measuring visually guided walking in naturally complex environments (e.g. as Matthis et al, 2018 have achieved with adults).

In study 2, we also found that both adults and children behaved cautiously when they could not plan at least 2 steps ahead. They demonstrated caution by walking more slowly and placing their feet more accurately. This contrasted with the findings of Matthis and colleagues who have used non-VR paradigms to consistently demonstrated that when adults are unable to plan ahead, foot placement error increases. Again, this contrast may be because in our VR task, participants had no peripheral visual input from their legs. Previous research has shown that when peripheral visual input from the legs is unavailable, adults behave cautiously by leaving larger margins between their feet and obstacles (Patla, 2008) and by taking shorter, slower steps (Marigold & Patla, 2008). However, we cannot be certain whether the cautious behaviour we observed in study 2 was caused by the VR set-up per se, or by some other aspect of the task. In future, more studies should seek to directly compare target-stepping and visually-guided walking behaviour in VR and outside of VR to robustly test the validity of VR tasks for understanding natural behaviour. VR is an extremely useful tool for scientifically testing behaviour in complex (yet rigorously controlled) environments. If we can further understand any differences between behaviour in VR and outside VR, we can be more confident in the conclusions we draw from VR studies going forward.

6.6.7 Online Control

In part 1, we drew a distinction between online control (using visual feedback to guide the current step into place) and feedforward control (using vision to plan the placement of a future step). However, even when pre-planning foot placement onto targets, vision is used continuously or ‘online’ for other purposes: to provide information about direction of travel, speed of movement, balance, and distance between the body and upcoming hazards, obstacles or targets (Gibson 1979; Marigold, 2008) There is much scope for future developmental research to further explore the nuances of online control in stepping and walking.

Firstly, in study 1 we found that children as young as 6 years use online vision to fine-tune precise stepping movements like adults. When vision was occluded at step onset, foot placement error was increased. However, based on this result we cannot be certain whether children need online visual feedback from the foot, the step target, the wider environment, or a combination of these sources to succeed at this task. In study 2, we administered a similar single precision stepping task. However, in this version, visual input from the foot and target was occluded at step onset, whilst vision of the wider environment remained. In this case, we found no main effect of vision on stepping performance. This suggests that children (and adults) may in fact be able to control precision stepping in a feedforward manner, providing they have continuous online visual input from the wider environment (perhaps to support balance control). To further understand whether children use online vision specifically to guide foot trajectory, future developmental studies should measure the trajectory of the foot during the stepping action. This approach was taken by Reynolds and Day (2005a), who found that adult steps follow a similar kinematic profile to visually guided reaches: an initial transport phase brings the foot into the general location of the target and visually guided adjustments to fine-tune the landing are made toward the end of the movement. This is a clear demonstration that online visual input is used to adjust the trajectory of the foot. Future studies should seek to perform a similar analysis of children's step trajectories with and without online visual input.

Secondly, in study 2 we contrasted the prediction that children would plan foot placement 2 steps ahead against the possibility that they would control walking one step at a time, using online vision to guide each step into place. Our results supported planning ahead as the preferred strategy of both 8-year-olds and adults. When participants could not plan at least 2 steps ahead, they slowed down and placed their feet more carefully. However, this feedforward approach does not preclude the possibility that children also need continuous, online visual information to guide other aspects of walking – such as distance and direction (Gibson, 1979; Marigold, 2008). Adult research has shown that adults can walk to pre-viewed targets up to 24 metres away relatively accurately without online vision, albeit in simple obstacle-free environments (Rieser, Ashmead, Talor & Youngquist, 1990). This demonstrates that in simple environments, continuous online vision may not be needed for controlling distance and direction of travel. However, future research should explore this both in children and in more complex terrain, reflective of the demands of cluttered everyday environments which pose additional challenges for balance and foot placement. In more complex environments, online visual information (e.g. about upcoming hazards) may be more important for controlling speed and direction of travel.

Finally, in this thesis we defined online control relative to the target and foot (online control being the visual guidance of the current step toward a target). Given that eye tracking research has clearly shown that adult walkers visually fixate future stepping targets (Hollands et al, 1995; Matthis et al, 2018), we could reasonably assume that this online control uses foveal (or central) vision of the foot and target. However, previous work has shown that adults also use online *peripheral* visual information about the legs to guide walking – for example in scaling steps over obstacles (Patla, 2008). Future developmental work should further explore the impact of both foveal and peripheral online visual input for children's locomotor control and could use eye-tracking methods to further clarify children's visual behaviour during walking.

6.6.8 Proprioceptive Tasks

In part 2, we focused on proprioception - in particular proprioceptive memory, exploring how well children could remember and reproduce limb positions. When learning new motor skills (like playing a sport, or getting dressed) children must coordinate their body and limbs into complex shapes. They must also remember and reproduce these complex whole-body shapes the next time they attempt a particular task. We sought to approximate at least some of this complexity in study 3 (by measuring proprioceptive memory for all four limbs separately) and in study 4 (by measuring children's ability to remember and reproduce complex, whole-body positions). However, this does present a challenge in that we cannot be sure whether performance is determined by proprioceptive ability, memory ability, or both. It is possible that children performed relatively poorly on these tasks because the memory component was too challenging. Had we measured proprioception per se in an 'online' task - such as limb position matching as used by von Hoftsen and Rösblad (1988) - children may have demonstrated stronger proprioceptive skill.

Previous studies have tested children's proprioception without memory demands and found that proprioception remains immature in late childhood and early adolescence (Goble et al, 2005; Holst-Wolf et al, 2016). This suggests that children's proprioception is maturing even into adolescence. Therefore, we might be confident that in studies 3 and 4 of this thesis, children's relatively poor proprioceptive memory performance was at least in part caused by immature proprioceptive ability (perhaps exacerbated by the memory demands of the tasks). It was a deliberate decision in the present research to test complex, whole-body proprioceptive memory – this highly complex behaviour is reflective of the demands of everyday movement and a steep learning curve for children. However, future research should seek to tease apart the extent to which performance on such tasks is explained by proprioception per se and/or by the memory demands. This could be achieved by administering additional tests of 'online' proprioception in its own right alongside complex proprioceptive memory tasks.

6.7 Thesis Conclusions

Using a whole-body approach, we have shown that sensorimotor development is protracted and asynchronous. Different sensorimotor skills develop and mature at different times, with both visually guided and proprioceptive control remaining immature in mid-childhood. Children's proprioception remains immature even in late childhood and early adolescence and lacks adultlike feedforward control mechanisms. In contrast, children show sophisticated and flexible use of visual information to plan and control movement. Children achieve adultlike visually-guided planning and control strategies before their movements have adultlike accuracy or precision.

Appendices

7.1 Appendix 1 - Constant Error

As an exploratory analysis, we calculated constant error (mean signed distance between target and participant's movement end-point: positive values indicate overshooting, negative values indicate undershooting). Here, we report the significant findings relating to constant error for children and adults.

7.1.1 Constant Error - Children.

With the arms, children undershot the target at large distances (*M*=-26.46mm, *SE*=5.38mm) to a significantly greater extent than at small distances (*M*=-5.99mm, *SE*=4.16mm), $F(1, 27)=18.06$, $p<.001$, $\eta p^2=0.40$, 90% *CI* [0.16, 0.56]. For the legs, children showed significantly more overshooting with the legs in the passive condition (*M*=16.30mm, *SE*=5.53mm) than the active condition (*M*=2.68mm, *SE*=3.97mm), $F(1, 17)=6.59$, $p=.02$, $\eta p^2=0.28$, 90% *CI* [0.03, 0.50]. This gives some small suggestion that, for the legs (but not the arms) children might benefit from forward models.

7.1.2 Constant Error – Adults.

With the arms, adults overshot targets at small distances (*M*=11.35mm, *SE*=3.04mm), whilst they undershot targets at large distances (*M*=-5.84mm, *SE*=4.14mm), $F(1, 19)=26.16$, $p<.001$, $\eta p^2=0.58$, 90% *CI* [0.30, 0.72]. We wanted to check that adults were not simply aiming for a central location (between the small and large distance targets) on every trial. To do this, we compared the distance moved on small distance trials and large distance trials. For this analysis, we scaled distance-moved to the average arm length of the scaling band. This was to account for the fact that participants moved different distances depending on their arm length. Because of this group-level scaling, the following analysis tells us *only* about whether the distance moved was significantly different for small vs. large distances. The scaled analysis does *not* provide useful information about error. We ran a repeated measures ANOVA (movement type x distance x dominance) on the scaled data. Adults moved their arms significantly further in the large distance condition (*M*=33.00% arm length, *SE*=0.78 % arm length) compared to the small distance condition (*M*=20.96% arm length, *SE* = 0.57 % arm length) $F(1, 19)=726.83$, $p<.001$, $\eta p^2=0.98$ *CI* 90% [0.95, 0.98]. Therefore, we rule out the possibility that adults aimed for a central location on all trials.

We also found an interaction among adults between movement type and dominance for constant error with the arms, $F(1, 19)=6.38$, $p=.02$, $\eta p^2=0.25$, 90% *CI* [0.00, 0.43]. Bonferroni corrected post hoc tests showed that for the dominant arm, adults' constant error was significantly higher in the passive condition (*M*=8.41mm, *SE*=4.50mm) than the active condition (*M*=-0.75mm, *SE*=3.48mm), $p=.031$. For the non-dominant arm, there was no effect of movement type on adults' constant error, $p=.82$.

For the legs, adults showed significantly higher constant error in the passive condition (*M*=15.30mm, *SE*=3.09mm) than in the active condition (*M*=4.23mm, *SE*=3.41mm) $F(1, 19)=11.83$, $p<.01$, $\eta p^2=0.38$, 90% *CI* [0.10, 0.57]. With the legs, adults overshot small distances (*M*=14.72mm, *SE*=2.96mm) to a greater extent than large distances (*M*=4.81mm, *SE*=3.20mm) $F(1, 19)=16.54$, $p<.01$, $\eta p^2=0.47$, 90% *CI* [0.17, 0.63].

7.2 Appendix 2 - Movement Time and Error Correlational Analysis

As predicted, we found significant effects of movement type on both absolute and variable error. Where we found significant effects of movement type (active/passive), we used correlations to examine whether these effects could be explained by target movement time: time taken for the participant to move from the start position, to the target, and back again during the target phase. This is because participants had free control over movement speed during the active condition, but not during the passive condition. We used non-parametric Spearman correlation because the sample sizes of these movement time analyses were small (due to equipment failure, movement time was not recorded for every trial). There were no significant correlations between absolute error or variable error and movement time for adults in the active condition (Table 7.1).

Table 7. 1

Spearman correlations between target movement time, and absolute and variable error for adults in the active condition.

	Absolute Error								Variable Error							
	Active															
	Dominant				Non-Dominant				Dominant				Non-Dominant			
	Small		Large		Small		Large		Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
p	.64	.72	.99	.06	.75	.84	.53	.59	.66	.65	.91	.39	.88	.18	.32	.89
r_s	.13	-.09	.00	-.50	-.09	-.06	.17	.14	-.13	.12	.03	-.24	.043	.37	.26	-.04
N	15	18	14	15	15	15	16	16	15	18	14	15	15	15	16	16

We also found a main effect of movement type for adults in our exploratory analysis of constant error. Therefore, we also calculated correlations between movement time and constant error. Again, no correlations were significant (Table 7.2).

Table 7. 2.

Spearman correlations between target movement time and constant error for adults in the active condition.

	Constant Error							
	Dominant				Non-Dominant			
	Small		Large		Small		Large	
	Arms	Legs	Arms	Legs	Arms	Legs	Arms	Legs
p	.41	1.00	.78	.37	.42	.44	.37	.58
r_s	.23	-.00	.08	.25	-.23	-.21	-.24	.17
N	15	18	14	15	15	15	16	16

Among children, we found a significant effect of movement type on constant error for the legs. Again, we wanted to check whether this effect of movement type could be driven by variation in movement time in the active condition. We calculated Spearman correlations between movement time and constant error. There was no correlation between children's movement time and constant error for the legs in the active condition (small distances - r_s = 0.01, p=.97, N=13; large distances - r_s = 0.43, p=.14, N=13

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